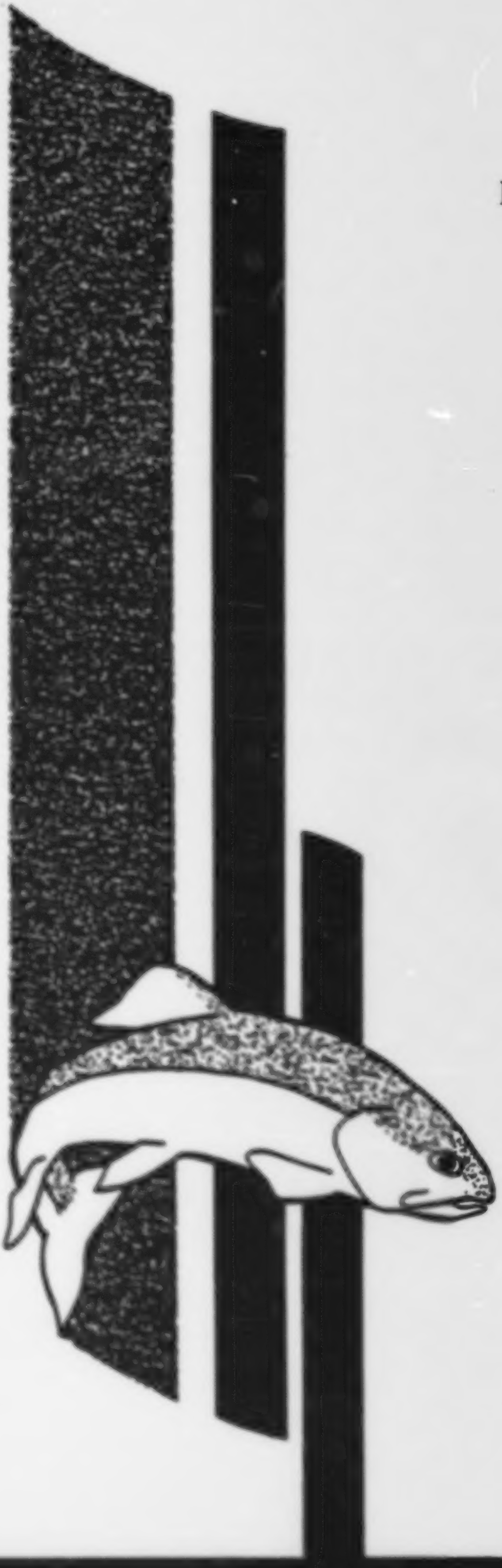

Feeding, Aggression and Growth in Juvenile Steelhead Trout (*Salmo gairdneri*)

by

JEREMY C. ABBOTT

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in the Department

of

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Simon Fraser University

December 6, 1985

JEREMY C. ABBOTT

15 April, 1957 - 27 September, 1988

Jeremy Abbott died "with his boots on"; he was killed in a helicopter crash while surveying spawning salmon in the Stuart River, near Vanderhoof, B.C. This tragic accident deprived us all of a good friend and a fine fisheries biologist. It was my privilege to have been his thesis supervisor at S.F.U. The research was done in co-operation with the B.C. Fish and Wildlife Branch.

At the time of his death, only two chapters of Jeremy's 1985 M.Sc. thesis had been published (Chapters IV and VI; see below). Other chapters of the thesis, which would have been published had he lived, are potentially of great interest and value to salmonid biologists, particularly those involved with high density rearing facilities such as net pens. With this in mind we've produced this copy of the entire thesis to make it more readily available to those who might benefit from the information it contains.

Jeremy was an avid steelhead fisherman, who was often heard to say that "there's no head like steelhead." He would be delighted if he knew that his research findings had been put to use to increase the numbers of the fish he loved so much.

Lawrence M. Dill

Thesis Publication History

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ABSTRACT

Abbott, J.C. 1991. Feeding, aggression and growth in juvenile steelhead trout (Salmo gairdneri). Prov. B.C. Fish. Tech. Circ. No. 93:110p.

Juvenile steelhead trout (Salmo gairdneri) compete for access to space and food, and the distribution of these resources within a population affects the relative growth and survival of individuals. Aggression is a means of competing for these limited resources. This thesis examines the causes of aggression and growth depensation (size divergence) in juvenile steelhead. The sizes of socially isolated juveniles diverged less with time than those of groups of interacting steelhead, although average growth rates were equivalent, indicating that the presence of competitors affects relative growth. A behavioural mechanism resulting in unequal food acquisition or growth efficiency is indicated, as rations were in excess of requirements. Size-matched pairs of steelhead established hierarchies in which dominants grew 12.3% faster than subordinates although rations were equal. Therefore factors other than access to food (possibly stress) play a role in growth depensation. Groups of steelhead grew faster when the inter-feeding interval was reduced, even though daily ration was constant. Size divergence over time was unaffected at intervals ranging from 0.5 to 24-h. Marked increases in aggression were consistently observed following feeding. The magnitude of post-feeding peaks was inversely correlated with inter-feeding interval. Total daily aggression and frequency of various behaviours were unchanged. Learning of feeding times and anticipatory aggression were demonstrated by recording behaviour on the fifth day of a feeding schedule and continuing to monitor behaviour for one day after feeding was discontinued. Alpha and beta hierarchy positions were stable over a one week period.

Underwater observation of steelhead in hatchery production facilities confirmed the occurrence of aggression. Various feeding regimes were presented to groups of steelhead in these facilities. No differences in growth, size divergence or fin damage were detected at four regular feeding intervals. Randomly fed fish showed less size divergence than regularly fed fish but had equivalent growth rates. This reduced growth depensation could result in a 6% increase in smolt production. Trout fighting tactics varied depending on the response of the opponent. Analysis of aggressive attacks and patterns of fin damage indicate that agonistic behaviour is the major cause of fin damage observed in culture facilities.

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I would like to thank Dr. Larry Dill for his equally rigorous attention to both general principles and detail, his critical support and friendship over the last five years. My committee members, Dr. G.H. Geen and P.A. Slaney provided useful advice, and Dr. R.M. Peterman commented on the initial stages of the study. Drs. R.L. Dunbrack and R.C. Orr discussed this project and its place in the universe at great length and assisted with several facets. All laboratory work was totally dependant upon the expertise of Rich Hotson and especially Alex Fraser. Dr. Des Mahon provided advice on the physiology of stress and means of avoiding it. M.J. Abbott assisted with many phases of the study.

I wish to thank all the Dillerians, present and past for discussions and their support: Drs. Louis Giguere and Ron Ydenberg, Kate Puckett, Wayne Donnelly, Mark "H." Abrahams, Peter Nonacs, Guy Martel, Ralf Carter, Rae Suttie and P.E. Bradshaw.

This study would not have been possible without the friendly and expert assistance of the B.C. Fish and Wildlife Branch staff: Dr. Art Tautz, P.A. Slaney, Graeme Lennie, Bob Land, Larry Mitchell, Bob Hooton, Lew Carswell, and Bill Harrower.

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I. INTRODUCTION

The survival and growth of stream-dwelling salmonids is largely density dependent due to the effects of territoriality and aggression (Chapman 1966, McFadden 1969). Young salmonids use aggressive displays and attacks to obtain a feeding territory, or a share of a food supply through membership in a hierarchy. Continued stream residence may be dependent upon success in behavioural interaction and failure may result in decreased feeding and growth opportunities, and increased physical damage and exposure to predators (Chapman 1966). This intraspecific competition is also of concern to the science of fish culture. Juvenile steelhead (anadromous rainbow trout, Salmo gairdneri) and other salmonids are cultured to smolt stage in high density tanks, ponds, raceways and net-pens to supply food and sport fishing demands for returning adults. It has been suggested that the problems of growth depensation[1], physical damage, stress and disease may be caused by aggressive behaviour (Chapman 1962, Yamagishi 1962, Fenderson and Carpenter 1971, Slaney and Harrower 1981) and may result in reduced production or in decreased post-release survival of hatchery raised fish. Thus, an understanding of the nature and determinants of aggression is important to the management of both wild and hatchery populations.

Aggression in animals is an adaptive behaviour which may be considered to have 3 major ends:

1. acquisition of object resources (food, nest material, shells, hosts) (Chapman 1966),

2. acquisition of other organisms for reproduction (mates), or labour (slaves) (Dawkins 1982),

3. avoidance of predation by ensuring access to refugia and escape routes, or by spacing (e.g., Donnelly and Dill 1984).

Alternatively, none of these items may be directly contested, but the space which contains them may be. If space or some requisite contained in that space, such as food or cover, is a limiting factor, competition may be operating. Ritualized displays may replace direct conflict for the area containing a resource (Chapman 1966), or position in a hierarchy may be contested (Barnard and Burk 1979). Thus, territorial or hierarchical aggression is an intermediary economical convention preventing the uneconomical contest of every food item regardless of location.

Although cooperative behaviours such as schooling and fright-huddling (Mason and Chapman 1965) are part of the behavioural repertoire of juvenile salmonids, most social interaction consists of agonistic, dominance-subordinance relations (Noakes 1978). Rank is defined by the outcome of conflicts for space or a share of space. Territoriality is defined here as strictly site-dependent dominance; hierarchies as site-independent interactions. These definitions are not exclusive and intermediate social systems exist, such as partial territoriality, where a fish defends a territory only against fish lower in the hierarchy (Noakes 1978). Since territory is maintained, delineated, and identified by the occurrence of aggression, the level of aggression has been used as a measure of the strength of territoriality (Dill et al. 1981, McNicol and Noakes 1984). However, because hierarchies are considered to be a strong social mechanism for the reduction of aggression (Barnard and Burke 1979), strength of the hierarchy may not be reflected in overt aggression. The theory of behavioural options and strategy in hierarchies has not been elaborated to the degree that it has for territorial systems.

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[1] the increase in variance of a size-frequency distribution with time due to differences in growth rates (Magnuson 1962)

The major factors governing the degree of territoriality or hierarchy that develops appear to be water current, density and size distribution of the fish. Observation of wild salmonids shows that territorial systems tend to occur in riffles among fish of uniform size. At a critical upper density, however, some territories collapse and former territory holders live as subordinates on or between other territories or are ejected from the system (Kalleberg 1958, Symons 1971, Slaney and Northcote 1974). This may indicate the existence of a minimum critical territory size. In pools, confined spaces (e.g., aquaria), and among populations of different-aged fish, hierarchies, despotism and partial territories occur (Newman 1956, Hartman 1965, Jenkins 1969).

The relationship of aggression and territoriality to feeding in juvenile salmonids has been recognized and investigated by a number of authors (e.g., Newman 1956, Keenleyside and Yamamoto 1962, Mason and Chapman 1965, Symons 1968, 1971, Slaney and Northcote 1974, Dill 1978a, Dill et al. 1981, McNicol and Noakes 1984), but equivocal results have been obtained. For example, some workers (Newman 1956, Kalleberg 1958, Keenleyside and Yamamoto 1962, McNicol and Noakes 1984) found increases in aggression after feeding while others (e.g., Symons 1968) found an overall decrease in aggression after feeding. While the effect of ration has been investigated, the timing of food presentation and the key question of how fish assess their trophic environment have not been considered.

Of the three causes of territoriality listed, juvenile anadromous salmonids are mainly affected by numbers one and three. The main function of stream rearing in the life history is growth and survival to an appropriate size and time for smolting. Acquiring territory or rank has been demonstrated to be strongly associated with survival, and an individual's feeding success and growth is closely related to its ability to hold a territory.

Atlantic salmon (Salmo salar) that do not hold a territory are attacked by territory holders if they attempt to feed or hold against the current (Kalleberg 1958). Brown trout (Salmo trutta) that could not maintain territories and were artificially prevented from emigrating lost weight and starved (Le Cren 1965). Chapman (1962) and Mason and Chapman (1965) have demonstrated that early downstream emigration in juvenile coho (Oncorhynchus kisutch) is a result of failure to acquire space through aggressive interactions. Although the fate of these migrants is unknown it does not appear that any return to the parent stream as adults. All returning adult steelhead trout and coho salmon appear to have spent at least one full year in freshwater, as indicated by scale readings (Maher and Larkin 1955, Chapman 1958, Bilton 1978). Thus, early migrants may have a limited chance of contributing to the next generation's gene pool.

In hierarchies the amount of food eaten and growth rate are closely related to position in the dominance order. Salmonids that hold low ranks exhibit less growth, higher mortality and more fin damage than higher ranking fish (Brown 1946, Yamagishi 1962). Growth depensation is generally attributed to differential food intake due to aggressive competition (Magnuson 1962, Yamagishi 1962) and indeed in cultured populations is taken as symptomatic of the occurrence of aggression (Jobling 1985). In addition, indices of stress, including plasma cortisol concentration, interrenal nuclear diameter and tailbeat frequency, are more evident in subordinates in small laboratory populations of coho parr (Ejike and Schreck 1980).

Territory holders and dominants may suffer less predation. A refuge and use of habitual escape routes were observed to be significant features of wild salmonid territories (Newman 1956, Jenkins 1969, Bachman 1984). Atlantic salmon parr that had established territories were less susceptible to brook charr (Salvelinus fontinalis) predation than parr which had not established territories (Symons 1974).

The economic dependability theory (Brown 1964) states that a territory should only be defended when the energetic gains of territory ownership exceed the costs. This simple statement is the basis of later, more elegant models describing and predicting when territories should be held and what size they should be. That animals are capable of adjusting territory size in response to changes in food availability and costs of defense is a fundamental concept of modern territory theory (Dill 1978b, Ebersole 1980, Hixon 1980, Schoener 1983). These authors have expanded upon Brown's (1964) concept of economic defendability by explicitly considering factors that influence territory size such as body size, food density, competitor density and travel costs. Hixon (1980) notes the different territorial requirements of energy maximizers and time minimizers and predicts that given an increased food abundance an energy maximizer will contract its territory.

Dill (1978b) and McNicol and Noakes (1984) consider juvenile coho salmon and brook charr, respectively, to be energy maximizers. Juvenile rainbow trout and coho salmon conformed to Hixon's prediction through decreased aggression with increased food availability (Slaney and Northcote 1974, Dill et al. 1981); however, these are the only studies that showed complementary responses of reduced territory size and decreased aggression. Other studies leave confusion as to mechanism and the possibility of alternative effects. To be capable of adjusting territory size in response to changes in food density, animals must be able to evaluate the status of their food supply. Because juvenile salmonids rely largely on drift, and hence, on allocthonous food sources (terrestrial or upstream production) it is unlikely that they are able to directly assess the production rate or standing crop of their food supply. It is more likely that past feeding history or present feeding status cue the behavioural decisions of salmonids.

Conflicting results in studies of salmonid feeding and aggression appear to stem from different measures of aggression, feeding schedules, and densities. The effects of competitors on growth, and whether through food monopolization or other mechanisms have not been determined. How aggressive damage occurs, and the risks and costs of aggression, have not been determined either. Research and hatchery feeding schedules and intruder pressure are typically very different from those found in nature. Other factors that affect energy budgets and aggression, competitor density and predator occurrence are also altered. The ability to monitor food supply is a requirement for optimal behaviour in a variable environment (Krebs 1978). Thus, timing of feeding may affect the perception of environmental quality, and hence aggression.

Steelhead trout are an important sport fish having economic and aesthetic value. Due to heavy fishing pressure and declining habitat they are cultured in hatcheries and, more recently, in floating lake pens (S.E.P. Annual Report 1979). Phenomena such as growth depensation, fin damage, disease and general stress which may interfere with production are likely to be aggression related (Slaney and Harrower 1981). In culture facilities the discrepancies in growth rates arising from social behaviour result in high growth depensation requiring labour-intensive grading (Bardach et al. 1972, Gunnes 1976). Almost no behavioural investigations have been performed on net-pen stocks of salmonids, yet there are potential benefits to be gained from an understanding of aggression and its effects.

Goals:

The purpose of this study was to investigate aspects of juvenile steelhead growth in relation to social behaviour and food availability. Figure 1 displays a conceptual model describing

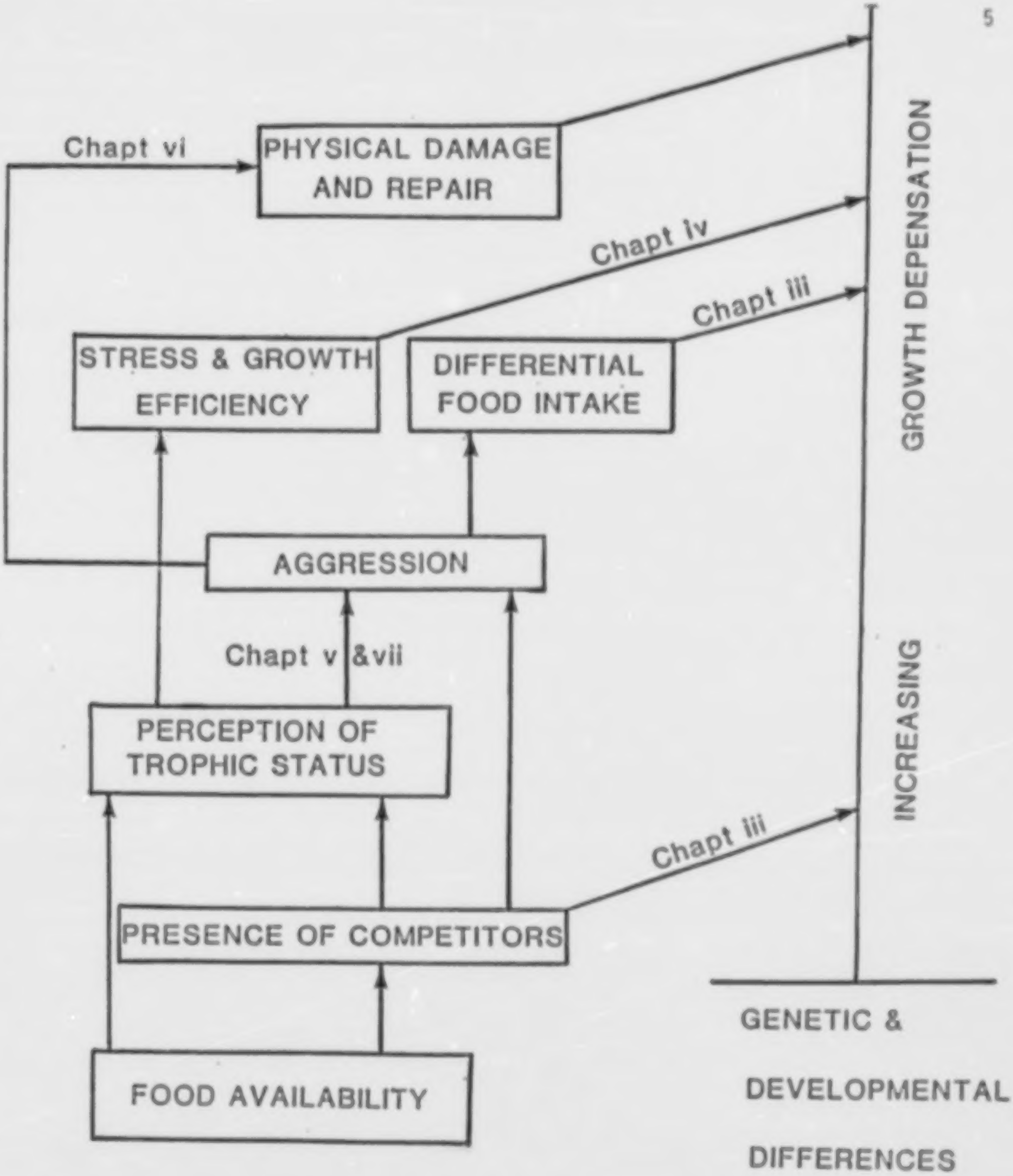
Chapt vi
PHYSICAL DAMAGE AND REPAIR
Chapt iv
Chapt iii
STRESS & GROWTH EFFICIENCY
DIFFERENTIAL FOOD INTAKE
AGGRESSION
Chapt v &vii
PERCEPTION OF TROPHIC STATUS
Chapt iii
PRESENCE OF COMPETITORS
FOOD AVAILABILITY
INCREASING GROWTH DEPENSATION
GENETIC & DEVELOPMENTAL DIFFERENCES

Figure 1. A conceptual model illustrating some of the factors causing growth variability in fishes.

possible factors that could influence growth variation.

Specifically the goals were:

1. to confirm that aggressive behaviour occurs in pen-held populations of juvenile steelhead (Chapt. II);
2. to determine if the presence of conspecifics is a major cause of growth depensation (Chapt. III);
3. to determine if reasons other than inequitable distribution of food are responsible for growth depensation (Chapt. IV);
4. to determine if different distributions of food over time produce changes in aggression and corresponding changes in growth depensation (Chapts. III and V);
5. to determine the relationship between observed attack patterns and observed fin damage (Chapts. VI);
6. to determine if juvenile steelhead are capable of learning feeding times and if they exhibit anticipatory aggression (Chapt. VII); and finally
7. to test a variety of feeding regimes in net-pen and hatchery populations in an attempt to reduce growth depensation and fin damage without a loss in growth rate (Chapt. VIII).

II. PEN OBSERVATIONS

METHODS

To gain a perspective of fish activity in floating net-pens and to verify the occurrence of aggression, underwater observations were made in rearing pens at a B.C. Fish and Wildlife Branch facility at Cowichan Lake, Vancouver Island. Initially I hoped to analyze the data quantitatively, but a review of the material indicated that the number of confounding factors (season, water temperature, fish size, age and density, dive time and feeding regime) and the infrequency of behavioural acts, rendered analysis meaningless. Therefore, only qualitative descriptions and ranges are presented.

Observations were in four pens (3.66m X 3.66m X 3.66m) suspended within a floating dock, covered with wire mesh lids and surrounded underwater by a wire mesh predator screen. Between October 28, 1980 and December 3, 1981, the site was visited 5 times with 4-6, 20-40 min dives taking place on each trip. Fish size ranged from 7 to 58 g, water temperature from 5 to 18 C, density from 2200 to 4000 per pen (44 to 80/m^3) and feeding intervals from 20 min to 2 hours, with supplemental hand feeding during some dives.

Observations were made with SCUBA apparatus. A rope sling supported the observer at a depth of 2 m without buoyancy concerns. Because systematic observation and recording was made difficult by the numbers and speed of the fish, a reference point (clear plexiglass with a blue circle) was suspended in the centre of the pen with monofilament. The first five minutes of each dive was spent waiting for the disturbance to subside. Thereafter focal animals (Altmann 1974) were selected by choosing the fish nearest to a reference point (the disk or a corner of the pen) and following it as long as possible. Records were kept on a plexiglass slate with a grease pencil and time intervals were signalled to the observer by an assistant pulling on the support ropes every 2 min.

OBSERVATIONS

Upon the diver's entry, juvenile steelhead exhibited a fright response, dashing about and crowding on the far, lower side of the pen. At this time especially the diver's exhalations had an effect on the fish as they moved towards and away from the diver in synchrony. In some cases it took over 10 min for the fish to recover. The typical pattern of fish distribution was characterized by having most of the fish milling in the upper central region of the pen. No characteristic clock-wise or counter clock-wise swimming was seen. Most fish swam horizontally and following initial disturbance came within 60 cm of the observer.

Fish in the lower central area appeared to be the largest fish in the pen.

Fish were sparsely distributed around the perimeter of the pen. These fish were mainly stationary and appeared to be defending a territory. One fish recognisable by a scar acted as if it were defending the diver's mask as reference point for a territory on two successive dives. This suggests that fish were only able to establish a territory with a spatial reference point and low intruder pressure, as observed in streams (Jenkins 1969). Conventional aggressive acts such as displays, charges, and chases (Mason and Chapman 1965) by territorial fish were observed, but no nips were seen in this context, apparently because intruders responded by fleeing.

Fish in the central area of the pen were densely packed (approximately 2-3 body lengths separation or less) and swam at relatively high speed. This inter-fish distance seemed constant regardless of the absolute numbers and size of fish. In contrast, the amount of open space about the periphery of the pen varied.

The following behaviours were observed in the centrally grouped fish:

1. Parallel swim: two fish would swim next to each other (3-6 cm apart) at high speed for a distance of 1-2 m;

2. Chases: one fish would swim closely and rapidly behind another, possibly attempting to nip its tail;

3. Charges: a high speed approach directed at another fish;

4. Bites: one fish would charge towards another generally from above and nip at the dorsum, usually at the dorsal fin;

5. Fights: a series of return nips between two fish.

In addition, fish sometimes swam stiffly, with exaggerated body motion and fins extended. Bites were normally made downwards after a charge of 2-3 body lengths. Several such vertical charge-bite sequences may occur in rapid succession. Fish that gave and received nips were often observed to turn sharply and rapidly downwards producing a visible flash.

Eroded dorsal fins were clearly visible both underwater and from above the surface. Fish in pens with relatively little fin damage were inconspicuous when observed from above the surface. In contrast damaged dorsal fins were visible from above as white lines. During feeding most fish swarmed towards the source to feed but the larger fish at the bottom remained there where food appeared to reach them. Activity and biting appeared to increase after feeding. Within a dive the number of acts recorded per 2 min observation period generally doubled for approximately 5 min following feeding.

Activity changed with season. Fish in winter were distributed deeper and were more wary. Aggressive acts were most frequent in late summer ($\overline{X}$=10 acts/2 min) and were negligible in January ($\overline{X}$=1.8 acts/2 min). These changes may have been related to changes in water temperature, photoperiod, fish size or density.

These dives established that aggression does occur in floating pens, and that nips occur and are directed towards the dorsal fin, which is the primary site of fin damage in hatchery steelhead. Few fish were conventionally territorial, probably because of spatial uniformity and high intruder numbers, but aggression occurred during all months. Flashing observed from above the surface may be evidence of aggressive activity but could be related to zooplankton feeding. Some relationship between feeding and aggressive activity appears to exist. However, the effectiveness of SCUBA observation was limited by the amount of time available due to air supply and temperature considerations, disturbance of fish, and the difficulty of observing large numbers of fish at this density.

III. RELATIVE GROWTH RATES OF ISOLATED AND GROUPED FISH FED AT DIFFERENT INTERVALS

INTRODUCTION

The occurrence of growth depensation in freshwater fish populations has been observed among wild juvenile coho salmon (Chapman 1962, Mason 1976), rainbow trout (Larkin et al. 1950) and largemouth bass, Micropterus salmoides (Shelton et al. 1979) and is common in hierarchies of laboratory fish and in hatcheries (Jobling and Wandsvik 1983). In nature, and artificial propagation facilities, growth depensation may result in significant losses of production due to cannibalism or failure to achieve a threshold size for survival (i.e., "smolt size") and in the case of hatcheries, in time costs of grading fish. Growth depensation may arise from genetic variability and/or early developmental differences, or from social causes such as food monopolization by dominants, differential energy expenditures, or social stress resulting from aggression. Although high relative growth rates are exhibited by behavioural dominants (Brown 1946, Yamagishi 1962, Li and Brocksen 1977), the role and mechanism of different social effects has not been determined.

Before considering social causes of growth depensation some estimate of the genetic/early development component should be obtained. Although growth depensation is commonly ascribed to social interaction, the critical comparison of the growth of individual fish, isolated from social effects, with the growth of grouped fish has rarely been made, and then only with small sample sizes.

In this study the growth variability of grouped juvenile steelhead (assumed to represent the summed effects of genetic, developmental and social factors) was compared to the growth variability of a sample of isolated control fish (assumed to be caused only by genetic and/or development factors). If social interaction is a significant cause of growth depensation, growth rates of grouped fish should be more variable than those of isolated controls.

In a second phase of the experiment, growth and behavioural observations were made of grouped fish fed equal daily rations, that were distributed differently over time. This was done to determine the relationships between food availability, aggression and growth. The growth of these groups is considered in the present chapter and their behaviour in Chapter V. Social interaction has been considered to cause growth depensation by several authors (Magnuson 1962, Yamagishi 1962, Jobling 1985), and several studies have shown that food availability affects aggression and territorial defence (reviewed in Dill 1978b). This chapter examines the effect of the temporal pattern of food availability, as measured by inter-feed time interval, on growth and growth variation. A range of regular feeding intervals within a 14-h photoperiod was examined. In addition a random feeding schedule, and one over a 24-h period were presented.

Due to the practical application of growth knowledge in stream and hatchery management, growth rates were considered in conjunction with growth variability. An optimal feeding regime would produce low growth depensation and a high growth rate.

METHODS

Juvenile steelhead trout (early winter-run Englishman River stock) were obtained from the Fraser Valley Trout Hatchery in 1981 and from the Big Qualicum Hatchery in 1982. All experiments were carried out at Simon Fraser University. Due to limited aquarium space it was not possible to run all trials simultaneously. As a compromise, I attempted to obtain fish as close to the initiation of feeding as possible, but due to brood timing this was not always the case. Table 1 gives the size and approximate age of fish used. The groups of steelhead usually hatched over a 7 day period.

Fish were initially held in 136-1, flow-through, aquaria until it was ascertained that they would feed, and then starved for two days prior to weighing and sorting. Water temperature throughout all experiments ranged from 8 to 11 C. A 14-h photoperiod (95 lx at the water surface) was used in all growth experiments; otherwise a natural photoperiod was generally maintained.

Fish were anaesthetized with methanesulfonate, and weighed to the nearest 0.1 mg on a Sartorius electronic balance after excess water had been removed with absorbant paper. Length was measured to the nearest 0.5 mm. After weighing, each fish was allowed to recover in an isolated vessel.

Experiments were conducted in 2 banks of 5, 45.5-1, flow-through aquaria for growth trial 1 and 2 and isolated control 1; a third bank of tanks was added for growth trials 3, 4, and 5, and isolated controls 2 and 3. Each tank had an exclusive dechlorinated water supply and an adjustable volume feeder (described by O'Keefe et al. (1979)). Each bank of 5 feeders was powered by a 1/15-hp electric motor. The feeders were controlled by a three channel timer capable of independently activating the drive motors at intervals from 1 to 999 min in 1-min increments. The feeders could also be activated at random intervals read from an internal list of 3000 numbers between 1 and 60 min. Thus each bank of 5 aquaria could be fed independently of the other 2, and each tank could be fed an independent ration size. Overhead lighting, which was necessary for videotaping was provided by 3, 75-watt incandescent floodlight bulbs per bank of tanks (2250 lx at the water surface).

TABLE 1. Source and use of experimental fish. All fish were winter-run Englishman R. steelhead.

Group	Date Obtained	Use	Approx. Age	Avg. Size (g)	T(C)
1	May 29, 1981	Isolated Control #1	Feeding +5 Days	.1814	8.0
2	June 23, 1981	Growth Trial #1	Feeding +24 Days	.2082	8.0
3	July 29, 1981	Growth Trial #2	Feeding +53 Days	.4279	9.0
4	Aug 9, 1981	Growth Trial #3	Feeding +123 days	1.279	10.0
5	June 1, 1982	Isolated Control #2	Feeding +5 days	.1422	9.0
6	July 3, 1982	Growth Trial #4	Feeding +20 days	.2344	8.0
7	July 27, 1982	Growth Trial #5	Feeding +10 days	.2178	9.0
8	Aug 11, 1982	Isolated Control #3 (Sequential)	Feeding +25 days	.2988	11.0

Isolated controls:

Three controls were conducted in which fish were socially isolated by black polyethylene on the back and sides of the aquaria. Ten similar sized fish were selected for isolated control 1, and 15 for controls 2 and 3. Fish mortalities in control 2 (5 fish) were replaced. Losses in control 1 and 3 (1 fish each) were not replaced. Tanks were partitioned to allow equal swimming volume per length of fish (22.75 L for fish to 35 mm, 5.68 L for each additional 5mm length increment to 55 mm). "Silvercup" feed in the appropriate size was provided *ad libitum*. This was operationally defined as a condition in which food was constantly available floating on the surface. Tank bottoms were siphoned to remove debris every two days.

In controls 1 and 2 the fish were weighed at the beginning and conclusion of the trial. In trial 3 fish were weighed at two or three day intervals to determine the shape of the growth curve. Initially they were weighed by the method outlined above, but after three weighings a technique that did not entail repeated anaesthetization was adopted. Fish were captured in a dip net, excess water was shaken off, and the fish placed in a pre-weighed vessel of water. The vessel was covered to control evaporation. Vessel and water weight were subtracted from the total weight to give fish weight. Final weights in all trials were obtained after two days of starvation to avoid weighing food remains in the guts. Fish were then sacrificed and dry weights obtained after oven drying for 3 days at 40 C.

Grouped growth trial:

Large groups of fish (>150) were starved 2 days, anaesthetized, and weighed individually. Following weighing, fish were sorted into groups of 8, on the basis of similar weight. Cold branding (Everest and Edmondson 1967) was attempted to allow individual recognition but was unsuccessful as the fish were generally too small to withstand the technique. Groups were installed in the 45.5-l aquaria previously described. Tanks were partitioned to provide a constant volume of water per unit of fish length as described for single fish. Some of the larger fish in growth trial 3 exceeded this requirement (3 tanks). Screens of 5 mm mesh were placed in each tank 1.5 mm above the bottom. This allowed food and feces to pass through and limited the period of availability of food to slightly more than the time the ration would float, similar to a pen-rearing situation. The tank ration was 10% of wet fish weight per day ("Silvercup" feed in an appropriate size). Food presentation schedules and the order in which the trials were run are given in Table 2. Food availability (time which food floated) for each feeding regime was approximately equal (Table 3). Fish in growth trial 5 did not feed well, and results from one tank in each feeding regime were excluded due to high mortality.

Table 2. Order of presentation of feeding regimes.

Growth Trial #	Feeding interval
1	24h fed 1hr. after daylight 24h fed 1hr. before dark
2	24h fed 2hr. after daylight 12h fed 2hr. after daylight and 2hr. before dark
3	12h commencing 1 hr. after daylight 4h " 2h "
4	2h " 1h " 0.5h "
5	0.5h " 0.5h (avg.) random interval fed throughout a 1h 24 h day

Table 3. Food availability-the approximate time that food floated in each feeding regime.

Feeding Interval	Time Floating/Feed	Total/Day
24h	18 min.	18 min.
12h	8.5 min.	17 min.
4h	4 min.	16 min.
2h	2.5 min.	17.5 min.
1h	1 min.	14 min.
0.5h	0.75 sec.	18.8 min.
0.5h (random)	0.75 sec.	18.8 min.
1h (X 24)	0.75 sec.	18 min.

After 5 days of feeding fish were starved for two days. Wet weight, length, and dry weight were measured as previously described. Fish that died during this final starvation period were weighed as discovered.

Growth analysis:

Instantaneous growth was treated as behaving as a power of wet weight (W)

$$\frac{dW}{dt} = KW^x$$

where K and x are constants (Parker and Larkin 1959) and was calculated as:

$$G_s = \frac{W_t^{.33} - W_o^{.33}}{t}$$

(Iwama and Tautz 1981) where the growth slope G_s indicates the growth rate independent of fish size. Incorporation of temperature (T) into the model gives the growth coefficient G_c:

G_c & G_s

$$G_c = \frac{G_s \times 1000}{T}$$

allowing comparison of fish grown at different temperatures.

Growth variability was expressed as the coefficient of variation, (group standard deviation/group mean dry wt.)*100. The change in coefficient of variation (CV)

$$\Delta CV = CV_t - CV_o$$

and is abbreviated DCV in the rest of this chapter.

RESULTS

Growth rate of fish in isolated control 3 (Fig. 2) demonstrates the essentially linear nature of growth over a 24-day period.

Three of the initial 40 fish in all controls lost weight, seven died and five replacements were treated as a separate group, i.e., G_c was calculated using a different value of t. Some isolates did not feed at all and did not appear to have learned to feed upon hatchery food. The average growth coefficient of single fish in all controls was 0.877, comparable to the fastest growth recorded in the grouped fish treatments (Fig. 3). The average growth coefficient of grouped fish was 0.347, significantly lower than from that of single fish (ANOVA, $p<0.001$); G_c for single tanks ranged from 0.1396 to 0.92. Grouped fish exhibited a clear trend of higher growth rates at higher feeding frequencies except at the 0.5-h interval (Fig. 3); the feeding interval effect was significant (ANOVA, $P<0.001$). All regimes in growth trial 5 showed low growth rates in comparison with regularly fed fish (Fig. 3).

The DCV/5 days of isolated controls (2.46%) was significantly less than that of grouped fish (8.02%) (F-test of squared coefficients of variation, $p<0.01$, Lewontin 1966). Figure 4 shows the small change of the coefficient of variation over 24 days in isolated control 3. This was the oldest group of isolates and they appeared most adapted to feeding. There was no effect of feeding regime on DCV/5 days (Friedman's test, $p>0.05$) in grouped fish and no trend is obvious (Fig. 5).

The combination of a significant effect of feeding interval on growth rate and equivalence of DCV/5 days suggests that, for any growth increment, feeding regimes producing the fastest growth also produce the least growth divergence. To demonstrate this the ratio $DCV/|G_c|$ was plotted against feeding interval (Fig. 6). There is a marked, but insignificant trend (Friedmans test, $p>0.05$) of decreasing relative variation with shortened feeding interval. Thus, although fish size did not diverge from the mean differently over time, weights of fish fed more frequently tended to diverge less relative to growth. In other words the growth of frequently fed fish was less variable than infrequently fed fish if compared over any equal size increment. The $DCV/|G_c|$ ratios of groups in growth trial 5 were high relative to those of the regular regimes.

Mortality was generally low in all feeding regimes except in growth trial 5 where 20% died during the feeding phase, and several more died during the 2-day starvation phase of the experiment (Fig. 7). Within a feeding regime deaths usually occurred in tanks with the smallest and occasionally the largest average size. Mid-size range tanks rarely incurred mortality. High mortality tended to coincide with low growth rate and high $DCV/|G_c|$ suggesting that all three measures may be associated with a stressed population, specifically in growth trial 5. Results for growth trial 5 may therefore be confounded by this overall pattern of stress.

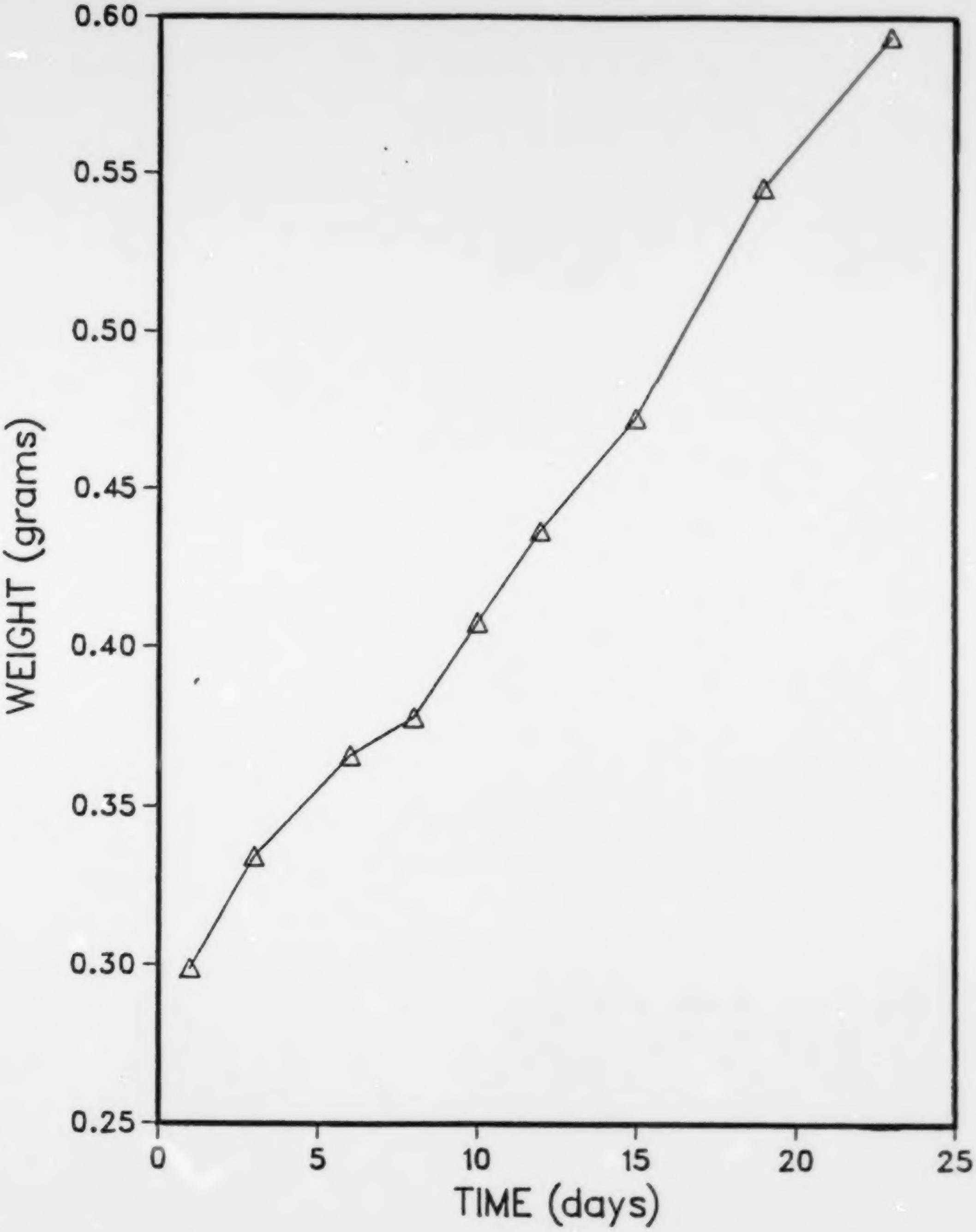

Figure 2. Sequential average wet weights of 14 isolated juvenile steelhead trout (isolated control 3).

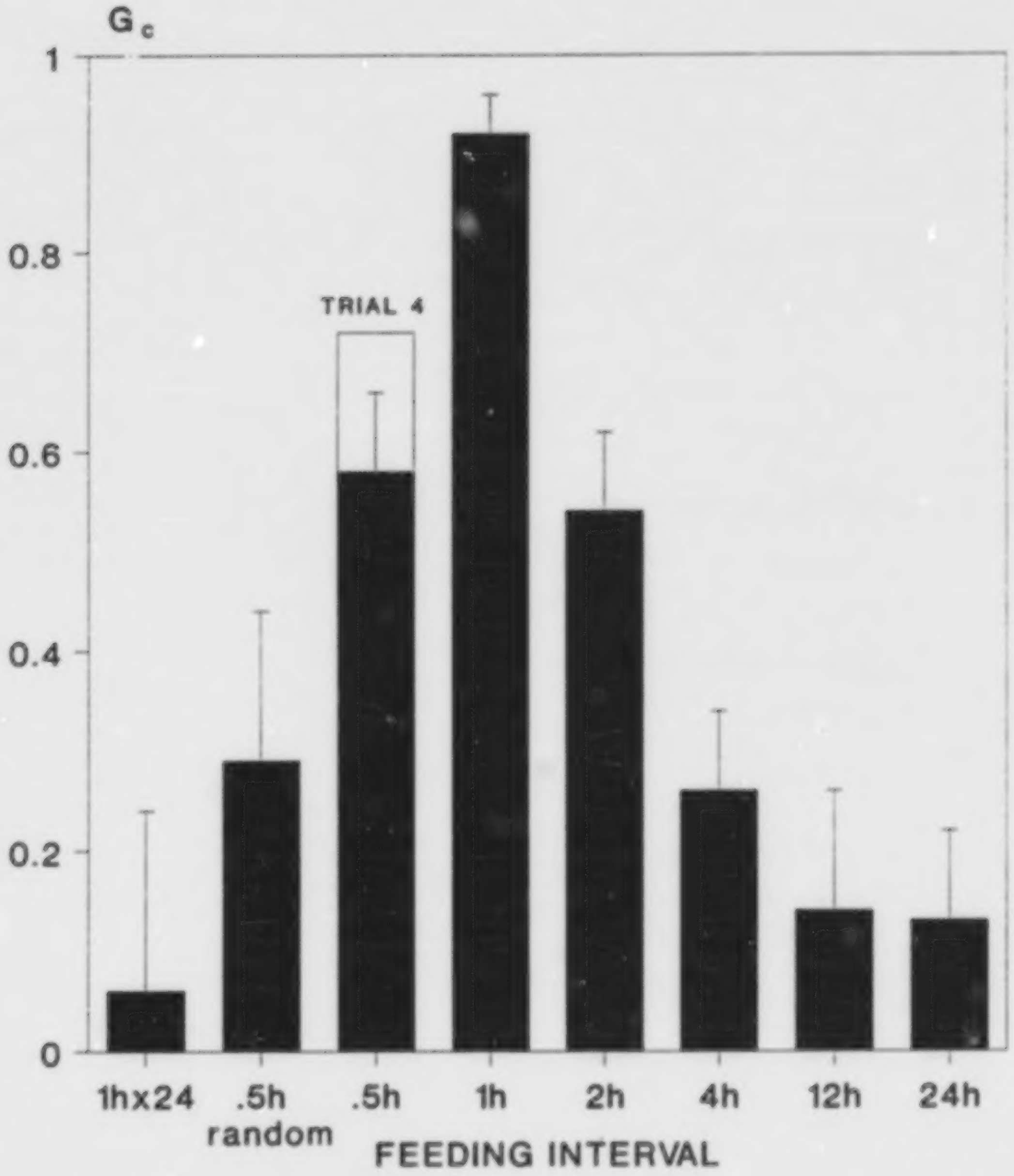

Figure 3. Average growth coefficient (G_c) of groups of eight juvenile steelhead trout under various feeding regimes. N (number of tanks) for each interval bracketed: 24h(15), 12h(10), 4h(5), 2h(10), 1h(5), 0.5h(9), random(4), 1hX24(4). Vertical lines represent standard errors. The open part of the bar at 0.5h represents the value for trial 4 alone.

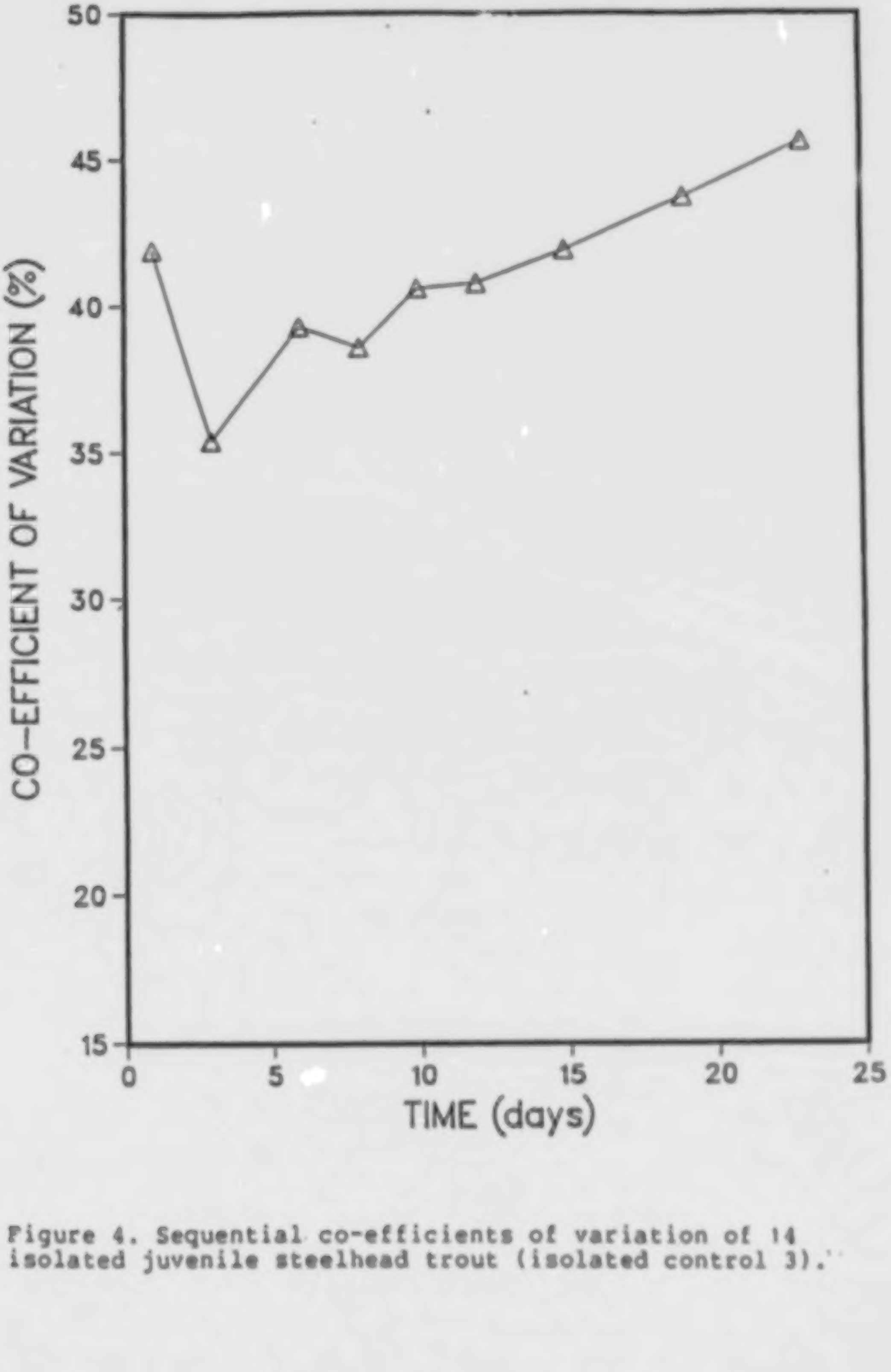

Figure 4. Sequential co-efficients of variation of 14 isolated juvenile steelhead trout (isolated control 3).

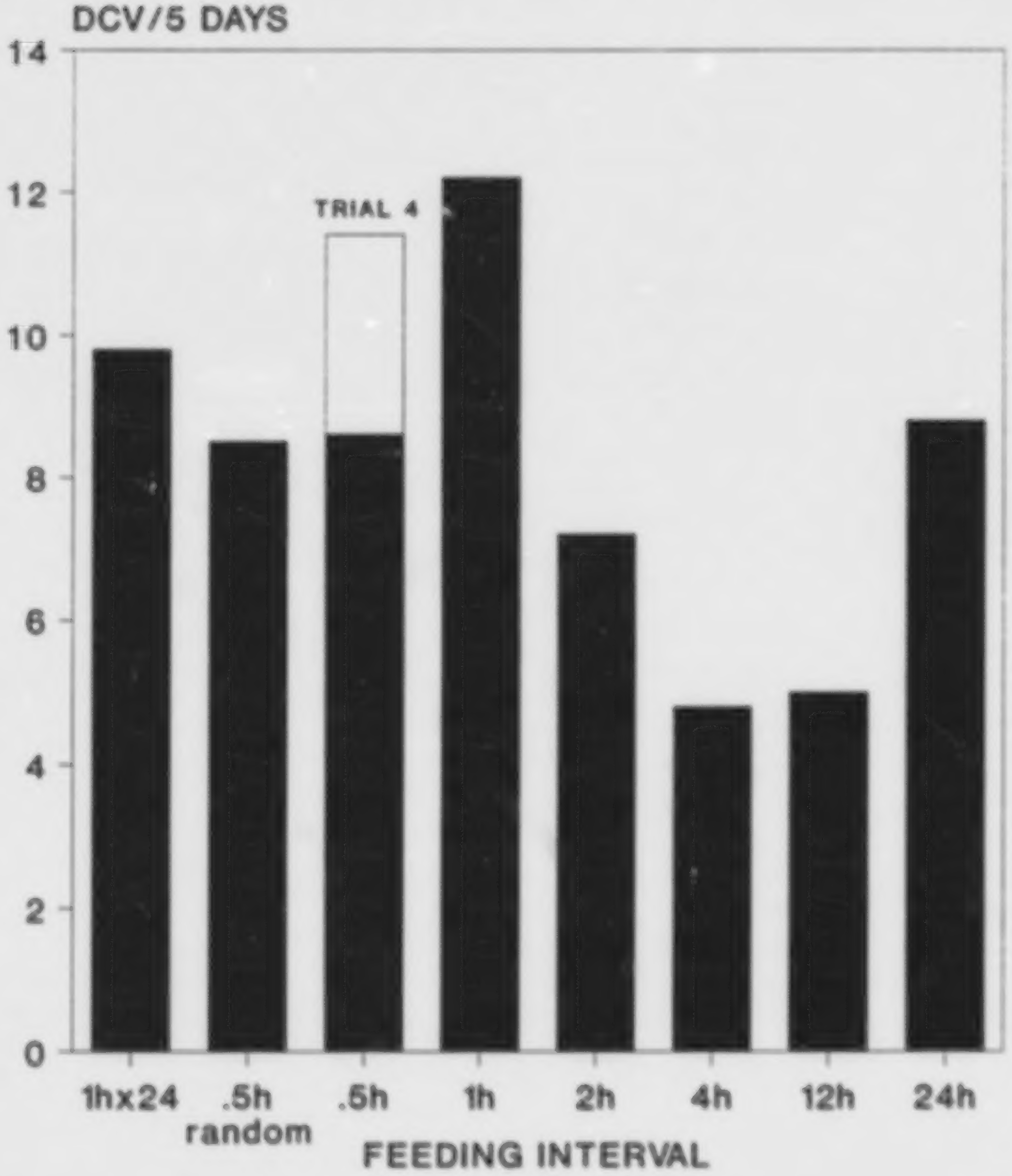

Figure 5. Average change in co-efficient of variation in groups of eight juvenile steelhead trout over 5 days. N as in Figure 3.

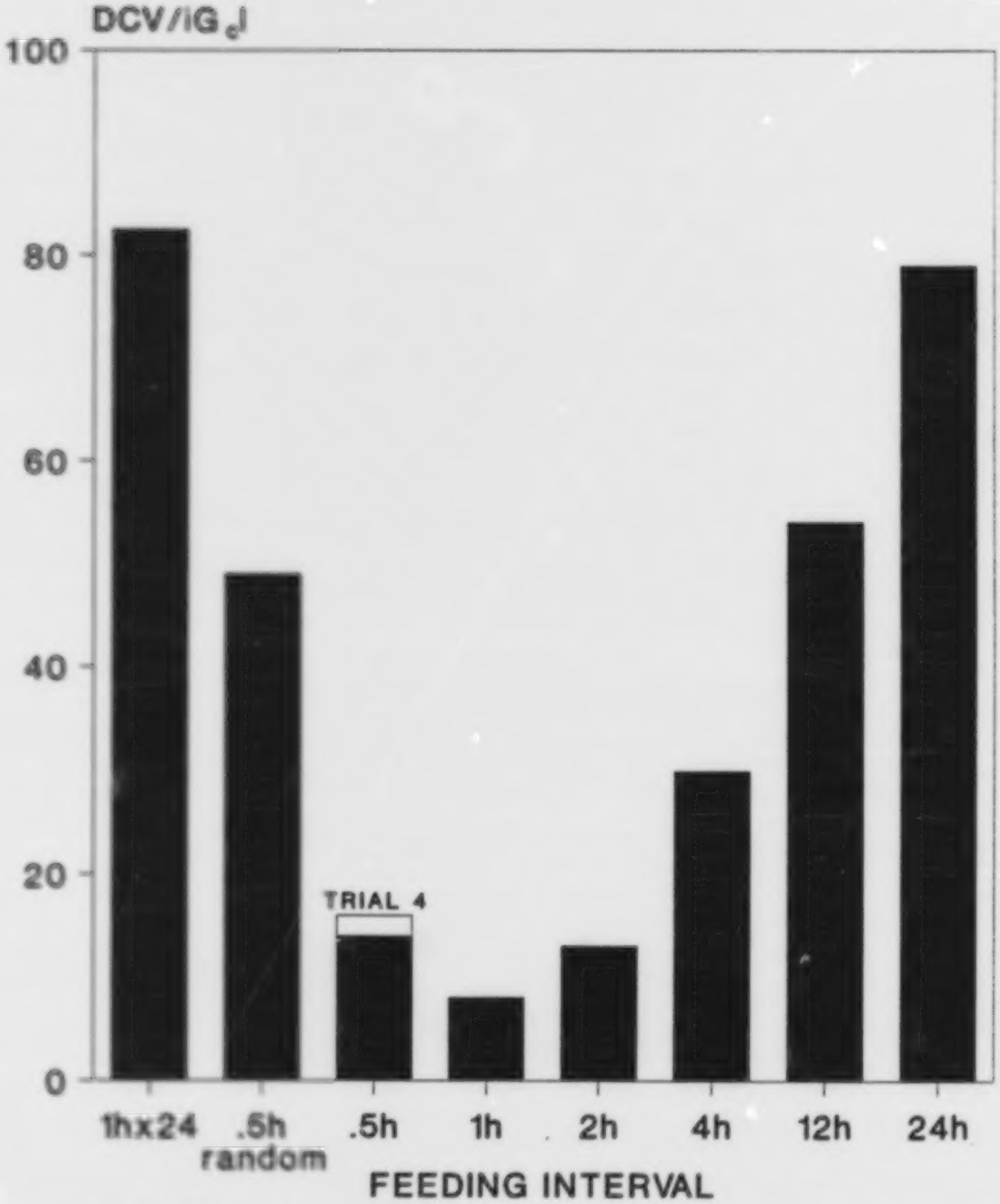

Figure 6. Change in co-efficient of variation relative to growth in groups of eight juvenile steelhead. N as in Figure 3.

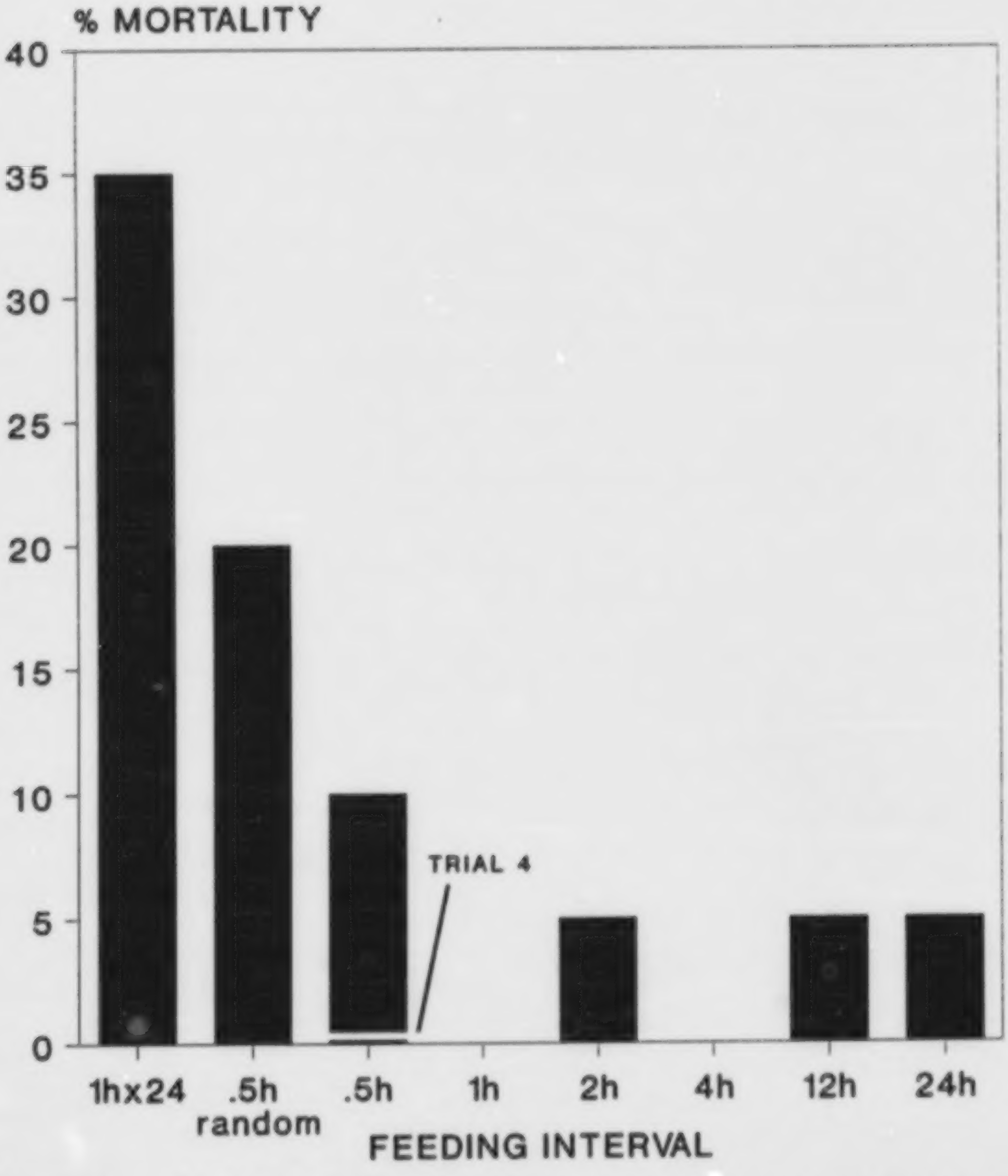

Figure 7. The occurrence of mortality in groups of eight juvenile steelhead. N as in Figure 3. The white bar at the 0.5 represents the value for trial 4 alone

DISCUSSION

Differences in growth performance were observed between isolated single fish and groups of 8 fish. Growth of single fish was comparable to that of fast growing groups and the growth rates of isolates were less divergent. Grouped fish generally grew faster with increased frequency of feeding and sizes diverged less for a given growth increment. The last growth trial, which compared a feeding regime of 0.5-h intervals, a random interval averaging 0.5-h, and a group fed every hour day and night showed low growth and high mortality.

The growth and relative size of juvenile fish relative to competitors is crucial to their future performance (Chapman 1962). In juvenile salmonids stream residence and territory ownership are size dependent, and the rank order of growth rate and access to resources often parallels that of size (Brown 1946, Mason and Chapman 1965, Yamagishi 1962) due to the success of larger fish in competition (Abbott et al. 1985). Survival during the stream-to-ocean osmotic transition is dependent upon reaching a threshold size (approximately 50 g in juvenile steelhead, Houston 1961). In fish culture facilities growth depensation means that large fish may obtain a disproportionately large share of resources, growing to an unnecessarily large size at the expense of a number of smaller fish. The smaller fish may be lost production if eventual production is limited by a size threshold. Examples would include a legally imposed size limit as in "put-and-take" stocking or a physiologically imposed osmotic threshold. If size gradients are large, "unexplained losses" (cannibalism) (Shirahata 1964) and labour cost associated with grading fish may be high. In addition, poor physical condition (emaciation, scale loss, damaged fins and scales) and elevated physiological stress indices are associated with low hierarchy standing (Brown 1946, Ejike and Schreck 1980). Thus, particularly in fish culture situations, the prevention of growth depensation may be as important as achieving high average weights.

The source of variability in growth rates within populations has been pursued along several lines of investigation. Genetic studies of full-and half-sib salmonids have assigned heritability values of 0.23-0.25 to growth rates (Gall and Gross 1978, Refstie and Steine 1978). These studies did not attempt to account for social interaction by isolating fish. More frequently, environmental and behavioural factors have been investigated as causes of growth depensation. Competition for food has been shown to influence levels of aggression and growth depensation. Several studies have investigated the energetic expenditures of fish involved in social interaction and made inferences about growth (Carline and Hall 1973, Li and Brocksen 1977, Puckett and Dill 1985). The occurrence of growth depensation has commonly been accepted as proof of the existence of energetically costly social interaction (Jobling 1985). However, without estimates of isolated individual fish growth, it can only be indirect evidence. The large space requirements for individual growth experiments generally prevent the rearing of large sample sizes of isolated individuals.

Before detailed consideration can be given to the present results and their implications, the methods and underlying assumptions should be discussed. Growth models used to analyze fish growth have been reviewed by Brett (1979). The logistic model is often used to represent the growth of organisms that initially grow quickly then slow down or reach an asymptote, as do determinate growers. The growth of young, fast growing, non-reproductive, indeterminate growers has often been analyzed with the use of the exponential model. Growth in both cases has been measured with a confusing variety of units and methods (Iwama and Tautz 1981, Jobling 1983). The model of Parker and Larkin (1959) accommodates the common observation in salmonids of declining growth rate (relative to size) with time (Shelborn et al. 1973, Elliott 1975). While most growth models are strictly empirical in that they describe without necessarily providing a functional explanation of the processes involved (Brett 1979, Peters 1983), Parker and Larkin (1959) suggested that the model could be partitioned into two major components -genetic and physiological potential for growth, represented by X, and ecological opportunities for growth, represented by K. K might represent such factors as temperature or ration size. Iwama and Tautz (1981) presented a method of comparing fish growth at different sizes and temperatures.

Because of the physiological consequences of low rank in a hierarchy (Ejike and Schreck 1980), dry weight should be a more accurate indicator of elaboration of tissue than wet weight. Characteristic loss of gill ATP-ase efficiency and impaired renal function in stressed fish impairs their ability to maintain osmotic homeostasis, and in freshwater fish results in an influx of water reducing percent dry matter (Mazeaud et al. 1977). Thus, the use of wet weight will cause an overestimate of the growth of subordinate fish. Percent dry weight should also increase with size independently of social rank due to increase in cell number and size (Weatherly and Rodgers 1978) and deposition of calcium as bone. All final dry weights obtained were regressed against final wet weight in an attempt to be able to predict initial dry weight on the basis of wet weight. However, due to low coefficients of correlation (r=0.41 in growth trial #1) and a reluctance to make assumptions regarding relative stress levels in the experimental groups of eight and the larger source groups, wet weight was used to express growth rates, in accordance with the model of Iwama and Tautz (1981). Individual identification of fish would have provided more information and required less inference about growth rates, however, as noted in Methods, cold branding failed and fin clipping might have altered competitive capabilities.

The size variation of isolated fish, relative to their mean size, was low in comparison to that of grouped fish. The average isolated growth rates were comparable to the highest grouped growth rates. The measure of DCV/5 days among the isolates was influenced by the fact that many isolated fish did not feed as extensively as grouped fish and that some isolated fish did not feed at all. Thus the measured DCV for isolates was probably an overestimate of the variation to be found among feeding and growing isolated fish. Non-feeding was probably due to one or both of two causes. First, fish may not have learned to feed on hatchery food prior to the start of the experiment. This would only be the case for very young fish since non-feeders would not survive to comprise part of the older groups. Secondly, non-feeding may have been caused by social and stress factors. Fish have been shown to exhibit social facilitation in their feeding, learning faster, feeding more vigorously, and growing faster when grouped than when isolated (Landless 1976). Thus, isolating fish that have had prior social experience cannot be said to have removed all social factors. Rather, after experience, isolation may be a condition of social deprivation that could increase observed growth variability. The first two groups of isolated fish were the smallest and youngest fish used in the study and had a higher incidence of non-feeders. The age and size of fish in control #3 was more representative of fish used in group trials. These fish showed minimal variability and I conclude that the results of control #3 are the most realistic. Data regarding growth variation of isolated individual salmonids have not appeared in the literature but general statements suggest that it is low (Yamagishi 1962, Li and Brocksen 1977). The present study appears to be the first to give sequential growth data on isolated salmonids. Koebele (1985) found the growth variation of isolated juvenile _Tilapia zillii_ to be lower than that of fish allowed to interact.

An increase in the coefficient of variation in groups of fish is generally considered evidence of social interaction (Magnuson 1962, Rubenstein 1981, Jobling and Wandsvik 1983). However, it is generally not stated that this argument holds only in the case of an unlimited food supply. Barnard and Burk (1979) have argued that any difference in vigour of competing animals in small groups is magnified by continued success. Hence increasing variability in growth or any other life history parameter influenced by energy acquisition, such as survivorship or reproductive output, is inevitable given unequal capabilities and limited resources. An increase in relative variability of growth in groups should indicate social interaction if food is provided in excess. Either behavioural dominants are excluding subordinates from food or subordinates are getting a full ration of food but are expending inordinate amounts of energy for maintenance or activity. The daily ration in the present experiments was twice that consumed in a single meal by other salmonids (juvenile sockeye salmon, _Oncorhynchus nerka_), following up 22 h of starvation, and exceeds the satiation range for most salmonids (Brett 1971). This confirms the importance of social interactions in determining growth in these groups of juvenile steelhead. There are numerous examples of despotic social systems in salmonids where dominants prevent subordinate feeding (Newman 1956, Keenleyside and Yamamoto 1962, Yamagishi 1962, Jenkins 1969, Symons 1971), and these observations were confirmed in this study.

That grouped fish grew faster at higher frequencies of food presentation, even with constant total ration, can be expected. Fish presented with excess food once per day were only able to eat until their stomach was full. Fish presented with food continually throughout the day, in the absence of competitive interference, would theoretically be able to fill their stomachs initially and then continue to eat at a rate equal to the gastric evacuation rate. Shelborn et al. (1973) found that continuous feeding for a 15-h day produced significantly greater growth in sockeye juveniles than feeding to satiation 3 times per day. Evidence of differing digestive efficiencies at maximum stomach loading and during starvation (Jobling 1982) indicates that the relationship between food intake and growth is not linear.

Poor growth performance in some groups was due to depressed growth rates relative to isolated fish. Fast growing groups had growth rates that were equivalent to isolates'. High variability in grouped fish was due to depressed growth rates of individuals, even to the extent of weight loss and death. Even in tanks whose populations grew slowly or lost total weight, dominant individuals achieved growth rates matching those of isolates and dominants in fast growing groups. Although growth depensation in crustaceans can result from increased growth rates of larger individuals relative to isolates (Ra'anan and Cohen 1984), the opposite is the common observation in fish. Jobling (1985) argues that a positive relationship between growth rate and size within a group is evidence of competitive social interactions.

DCV/5 days was not significantly affected by feeding regime. However, the growth differences discussed suggested looking at growth depensation relative to the magnitude of size change. In this case there was an obvious (although insignificant) effect of feeding interval. Because more frequent feeding provided statistically equivalent DVC/t in conjunction with increasing growth rates, frequently fed fish were actually diverging less in size over a given growth increment, i.e., for an equal size increase, more frequently fed fish would exhibit less growth divergence. However, it will take the different groups different times to grow that increment.

Growth depensation is usually measured relative to time. This assumes that growth does not vary in the populations being compared. Organisms adding biomass with the same variance would be expected to produce differing changes in the co-efficient of variation if grown at different rates for an equal time period.

Equivalent values of DCV/t only reflect equal divergence if referring to normally distributed populations growing at the same rate. Comparing rates of divergence for equal time periods relative to the size change (DCV/$|G_c|$) allows a more comprehensive evaluation of the population growth. This approach may be of more value to fish culturists where growth divergence relative to growth (and feed expended) may be more important than growth divergence relative to time.

Random and round-the-clock feeding gave poor performance in both DCV and growth rate. This may in part have been due to the entire group not getting a good start on hatchery food or being generally stressed. The concurrent 0.5-h regular feeding regime with fish from the same group also performed poorly and mortality in this trial was considerably higher than in other trials. Because fish that were losing weight would be more likely to die their loss would decrease the measured coefficient of variation. Randomly fed fish may have been less efficient at utilising food due to being unable to learn the delivery schedule. Results in Chapter VII indicate considerable accuracy in learning feeding times, and studies of demand feeding behaviour in rainbow trout show that only a short time is required for learning (Landless 1976). Regularly fed fish exhibited anticipatory behaviour immediately prior to feeding (Chapter VII) which may enable them to utilize food more efficiently. It was not possible to determine whether fish fed in the dark, but build up of uneaten food in tanks suggests they did not. This may explain part of the poor performance of fish fed through a 24-h day, since their effective total ration would be lower.

It is notable that high growth rates coincided with low DCV/$|G_c|$ and low mortality. This may indicate that all three parameters are general indicators of stress or health in a growing population.

In conclusion, this section of the study has shown that social interaction plays an important role in determining the relative magnitude of growth rates and is probably the major cause of growth depensation in juvenile steelhead. Temporal distribution of food also plays a role in determining growth rate and variability. The implication of these results to fish culture is that growth should be maximized by frequent feeding, at least once per hour. Variability in relation to growth will also be minimized by frequent feeding. Controlling these variables satisfactorily should also reduce morality.

IV. THE RELATIVE GROWTH OF DOMINANT AND SUBORDINATE FISH ON EQUAL RATIONS

INTRODUCTION

This experiment tests the hypothesis that relative dominance status dictates the relative growth of fish fed equal rations. Growth depensation due to differential growth rates is a common feature of fish populations, particularly in captivity (see Chapter III), and dominant fish exhibit superior growth rates relative to subordinates (Brown 1946, Yamagishi 1962, Li and Brocksen 1977, Carline and Hall 1973). A significant portion of this variation can be attributed to differential access to food. Dominants may defend point food sources or areas of high prey encounter rate (Yamagishi 1962, Wankowski and Thorpe 1979, Rubenstein 1981), thus interfering with the feeding of subordinates. Increased rations reduce growth depensation (Magnuson 1962, Koebele 1985), but high variation persists (Yamagishi 1962). These studies found that increasing the spatial dispersion of food, making it more difficult or costly to defend and equalizing access, leads to decreased growth variation.

An alternative cause of growth depensation is that subordinates may convert food to biomass (gross growth efficiency; Webb (1978)) less efficiently than dominants. Newman (1956) and Kalleberg (1958) suggested that reduced growth efficiency could be due to higher subordinate activity levels. Carline and Hall (1973) suggested that subordinates had higher metabolic rates, and Jobling and Wandsvik (1983) postulated an "undefined psychological stress" as a cause of growth depensation.

The complex of physiological conditions that occur in fish challenged by sub-optimal environments is generally referred to as the "stress syndrome" (Mazeaud et al. 1977). Some of these physiological parameters (e.g., increased corticosteroid production and distributed glucose metabolism) have been correlated with position in a dominance hierarchy (Erickson 1967, Noakes and Leatherland 1977, Ejike and Schreck 1980) and can be expected to influence metabolic rate.

I hypothesize that the energetic costs of relatively "stressed" subordinate fish should be higher than those of the dominant. These added costs should result in reduced growth relative to the dominant even if access to and consumption of food is constant. As a result subordinates should show a lower growth efficiency.

Access to food was controlled in size- and age-matched pairs of juvenile steelhead by separating fish briefly at feeding time, enabling them to consume equal rations. This ensured that the dominant had no advantage in obtaining food. It was predicted that dominants should grow faster than subordinates; this difference should be a measure of the metabolic cost of subordinance.

METHODS

Juvenile steelhead were obtained from the sources described in Chapter III. Fish for the present experiment were selected concurrently with the weighing of large numbers of fish as described in Methods, Chapter III. During the sorting process pairs most similar in size and length were set aside for use in this experiment. The twelve pairs obtained differed by no more than 0.0002 g (<0.001%) and 1 mm (usually within 0.5 mm).

Paired fish were placed in 45.5-l aquaria equipped with a removable, central, opaque divider. Dechlorinated water entered and drained from opposite ends of the tank and flowed through the tanks sequentially. Fish were randomly placed on the inlet or outlet side of the divider. Identifying characteristics of fish, such as fin and parr markings, were recorded during a 24-h acclimation period. The barrier was then removed and the fish allowed to interact. Dominance was assessed by the ability to deliver unreciprocated nips, unrestricted use of both sides of the tank, and typical rank coloration (Abbott et al. 1985). Fish that met all three criteria were considered dominant. Fish were fed equal maintenance rations (2-3% wet weight, live Tubifex spp.) during a short separation period until dominance was determined, usually within 2 days.

The experimental feeding regime ensured that there was no possibility of the dominant receiving a larger ration than the subordinate. Food organisms (various sizes of brine shrimp Artemia salina, fruit fly Drosophila melanugaster, and onion fly Hylemaya antiqua) were placed in size-matched pairs. Fish were separated by lowering the central divider and the subordinate was fed one prey item. If that prey was eaten then the dominant was presented with the matching prey. This was continued until either the subordinate or the dominant refused a prey item. Thus, the only possible disparity in ration level was that the dominant could refuse one prey item after the subordinate had fed. This occurred in 12 instances of a total of 798 feedings, with brine shrimp as the prey in each case. Fish were separated for less than 5 min per feeding period.

Fish were usually fed twice per day at 1000 and 1400 h. Initially, behavioural observations were made for 10 min immediately after the fish were reunited. After 11 observations of the first pair (these observations are not included in the data set) this was changed to 10 min before and after separation. When several pairs were run concurrently only one tank was observed per feeding. Nips, charges, chases, displays, and crosses of the tank centerline were recorded using a Datamyte 800 event recorder. The last behaviour was assumed to be a measure of ability to use tank space and search for food; it is also a crude index of activity level. Holding position and presence or absence of typical salmonid subordinate coloration were noted, and instances of fin damage were recorded. Experiments were ended when three observers independently identified the same fish as larger.

Fish were then separated, starved for two days to eliminate gut contents, and final measurements taken as in Chapter III. For the calculation of dry weight increases, paired fish were assumed to have equal percent dry weight at the beginning of the experiment, i.e., both fish were assigned the mean of their final percent dry weights.

RESULTS

Ten of twelve dominant fish grew faster than their paired subordinate whether growth was measured as wet or dry weight increase (Table 4), although the 10 fish with greater wet weight increases were not the same 10 fish with greater dry weight increases. The average daily growth of dominants was 0.51% initial dry wt/day greater than the average daily growth of subordinates (Wilcoxon matched-pairs signed ranks, $P<0.05$; Table 5). The growth rates of dominant pair members were 12.3% (range -9.9 to 46%) greater on average than the growth rates of their subordinate tank mates. Nine of twelve dominants contained a greater proportion of dry matter at the end of the experiment than did their paired subordinates (Table 5), but the difference was not significant (Wilcoxon test, $p<0.05$).

Dominants made greater use of the tank area by crossing the centerline of the tank more frequently, and committed more aggressive acts than subordinates (Wilcoxon test, $p<0.05$, Table 6). Subordinates received more fin damage than dominants (Fig. 8). Patterns of fin damage were similar to those described in Chapter VI, with most damage being to the dorsal and pectoral fins.

DISCUSSION

This study has predicted, and demonstrated, dominance-related differences in growth. Paired fish of virtually equal size fed equal rations grew at different rates; the average dominant grew faster by 0.51% dry body weight/day, representing a 12.3% advantage over the average subordinate in growth efficiency.

The similarity of size and age at the start of experiments minimized any difference in growth potential due to heredity or early developmental conditions, since both members of a pair had achieved the same growth under the same rearing conditions. As both members of a pair were the same age (within 7 days) this also suggests similar initial metabolic efficiencies. Previous social experience may strongly affect future competitive performance (Frey and Miller 1972, Francis 1983, Abbott et al. 1985), but individual recognition and previous experience within these pairs is unlikely due to the large hatchery source populations. Differential foraging ability or direct interference competition were not permitted to play a role due to the method of separate food presentation.

TABLE 4. Growth increments of paired juvenile steelhead in grams (* indicates pairs where subordinates grew faster than dominants).

Pair #	Wet weight Increase		Dry weight Increase		Days of Growth
	Dom.	Sub.	Dom.	Sub.	
1	.2387	.1824	.0415	.0306	40
2	.2914	.2104	.0536	.0377	46
3	.2196	.1656	.0382	.0309	29
4	.2157	.2063	.0413	.0368	29
5	.2005	.1995	.0370	.0375*	29
6	.1629	.1689*	.0275	.0303*	29
7	.2180	.1992	.0384	.0361	29
8	.3391	.3261	.0645	.0593	37
9	.3565	.3717*	.0687	.0664	37
10	.3465	.2970	.0621	.0528	37
11	.1390	.1169	.0240	.0194	37
12	.0826	.0762	.0133	.0113	27
$\bar{X}$	.2342	.2100	.0435	.0374	33.8

TABLE 5. Growth rates and final percent dry weights of paired juvenile steelhead (* indicates pairs where subordinates grew faster than dominants or had greater % dry weights).

Pair #	Growth rate % Dry wt./day		% Dry weight	
	Dom.	Sub.	Dom.	Sub.
1	3.72	2.74	17.3	16.9
2	3.71	2.62	18.3	18.0
3	5.90	4.80	17.6	18.4*
4	6.72	5.99	18.9	18.1
5	5.34	5.41*	18.5	18.7*
6	3.81	4.19*	17.1	17.6*
7	5.83	5.48	17.4	16.8
8	3.70	3.40	18.8	18.4
9	3.38	3.27	18.9	18.2
10	3.60	3.06	17.9	17.8
11	2.63	2.12	17.1	16.8
12	2.10	1.80	16.1	16.0
$\bar{X}$	4.21	3.70	17.8	17.64

TABLE 6. Aggressive and general activity of paired juvenile steelhead.

Pair #	Aggressive Acts		Crosses	
	Dom.	Sub.	Dom.	Sub.
1	12.4	2.6	8.5	2.6
2	25.9	8.4	17.6	4.7
3	10.4	0.8	12.5	8.3
4	11.6	3.2	15.8	2.9
5	11.4	1.8	12.7	1.9
6	3.5	1.5	3.5	1.8
7	3.9	0.1	4.0	0.2
8	11.8	6.8	3.8	1.9
9	4.2	0.8	2.4	0.4
10	8.3	1.8	0.8	0.0
11	2.8	0.3	2.0	0.4
12	11.7	1.0	9.6	0.9
$\overline{X}$	9.8	2.4	7.7	2.1

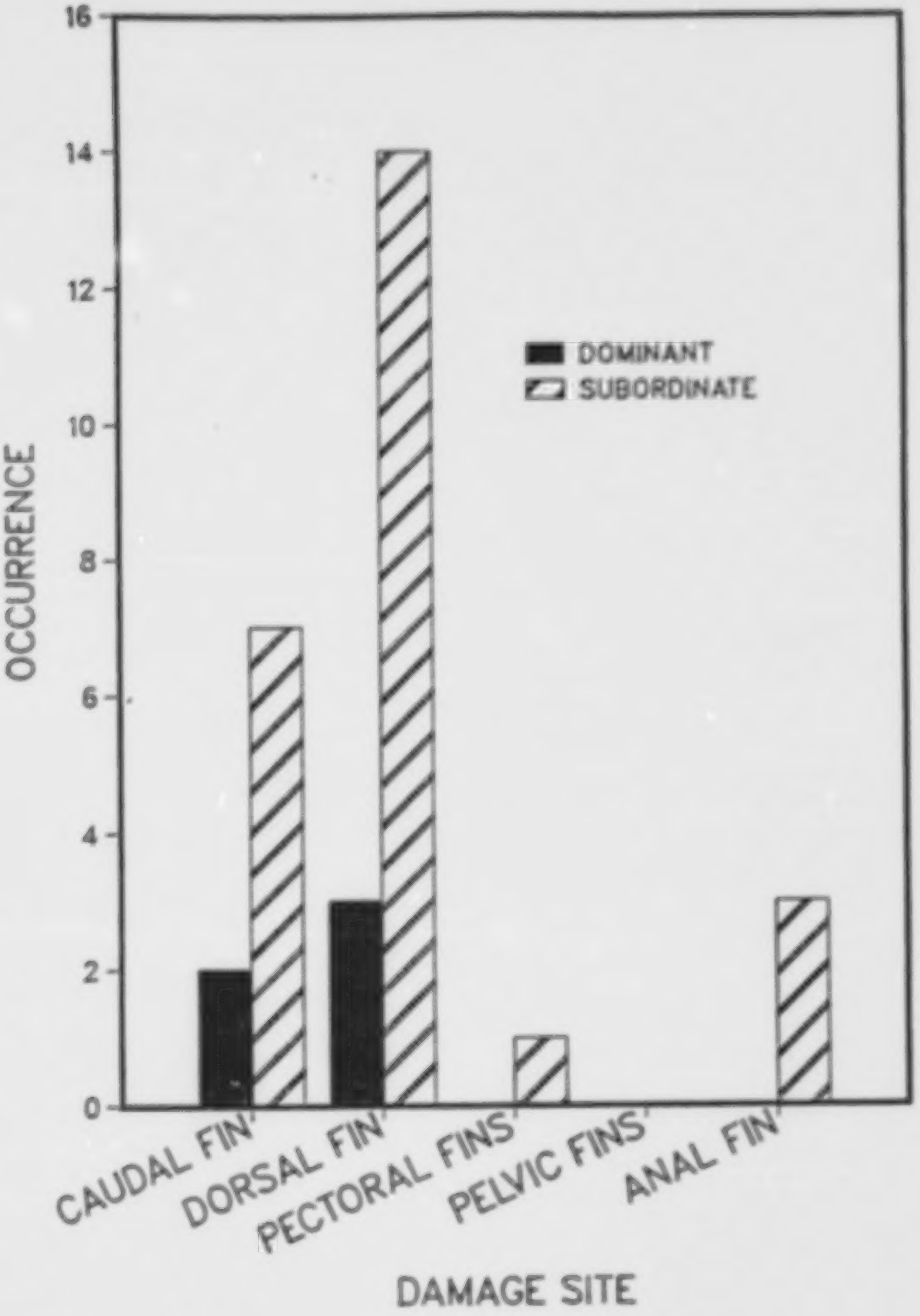

Figure 8. The occurrence of observed instances of fin damage in juvenile steelhead trout judged to be dominant and subordinate.

Koebele (1985) reared trios of juvenile Tilapia zilli which were fed equal rations while briefly separated. The growth variance of trios was the same as that of socially isolated individuals, but they displayed less variance than grouped fish that were competing for food. However, no predictions regarding relative growth and behavioural status were tested and behavioural observations were not reported.

Increased activity did not cause the low growth rates of subordinate steelhead. Behavioural observations of this study and others (Kalleberg 1958, Mason and Chapman 1965) indicate that increased movement associated with aggression and feeding are not generally correlated with subordinance. In fact, unless forced to faster currents, subordinates generally are less active than dominants. Li and Brocksen (1977), Carline and Hall (1973) and Ejike and Schreck (1980) found that high levels of activity and aggression were correlated with high food intake and growth efficiency. Jobling and Wandsvik (1983) hypothesized that "psychological stress" might cause starvation or reduced appetite. Highly stressed fish have been observed to cease feeding (Chapt. V) and subordinate fish have been shown to voluntarily reduce food intake (Abbott et al. 1985). In the present study subordinates always maintained an appetite, and consumed increasing amounts of food over the course of the experiment; it could not be determined if voluntary intake was lower than that of the dominant, however.

The most likely explanation for the results is that dominant status is associated with reduced costs, or conversely, that subordinate status is associated with increased costs. Rowell (1974) argues that a dominant is in a normal unstressed condition and that subordinate behaviour represents the measurable result of dominance interactions. Since dominant growth rates were comparable to maximum salmonid growth rates recorded in the literature (Brett 1971), and those of grouped fish recorded in other experiments (Chapt. III), depression of subordinate growth rates appears to be the likely cause of size divergence. Aggressive activity of dominants is reflected in the greater amount of damage sustained by subordinates. Repair of this damaged tissue should entail an added cost for subordinates.

Several behavioural and physiological indicators of stress are likely to be associated with higher energetic costs. Higher gill ventilation and fin beat rates suggest a higher rate of energy utilization or reduced energetic efficiency (Ejike and Schreck 1980). Efficiency of gill and renal osmotic functions is impaired as a result of increased corticosteroid production (Mazeaud et al. 1977), suggesting that more energy must be expanded to maintain homeostasis. The increased blood glucose levels resulting from mobilization of liver glycogen indicate that more energy is being used (Mazeaud et al. 1977), and high lactate levels indicate that glucose is being metabolised by relatively inefficient anaerobic pathways (Beggs et al. 1980).

An attempt to indirectly monitor stress parameters in this study was to measure percent dry weight. Due to decreased osmotic efficiency stressed freshwater fish may have a higher water content than non-stressed ones. For example, Ejike and Schreck (1980) and Fagerlund et al. (1981) have shown that dominants have higher percent dry matter content than subordinates. Most dominants in the present study had higher percent dry weights as expected, but the difference was not statistically significant.

How closely the stress levels of the experimental fish correspond to those of fish in natural conditions is not known. The fish did not appear to be stressed as severely as fish in hierarchies (Chapts. III & V) where some subordinates were observed to cease feeding and die. The subordinates did not suffer great physical damage, and were not held at high densities. Several studies of wild stream-dwelling salmonids and fish in stream channels suggest wild fish may be under stress. Subordinate juvenile coho salmon or floaters (non-territorial) have less access to food, may be forced to hold in disadvantageous positions, and are continually at risk of attack (Puckett and Dill 1985). Such situations and high density conditions resulting from low stream flows and hierarchy formation in pools may produce high levels of stress in the wild.

The advantage of territory ownership or primary hierarchy position, both examples of dominance, have been shown both theoretically and experimentally (reviewed by Gauthreaux 1978). Increased success at food, space and mate acquisition are examples of advantages of high social position. Most studies have concentrated upon these resource benefits that accrue to dominants, but dominant juvenile salmonids will engage in aggressive activity even when there is no apparent advantage in terms of resource acquisition. Examples include satiated dominants preventing subordinates access to food, and foregoing feeding to engage in aggression (Kalleberg 1958, Mason and Chapman 1965). The present results indicate that models based on time or calories transacted in feeding or defence of territories (Dill 1978b, Hixon 1980, Schoener 1983) underestimate the advantage of territory ownership. These models assume that costs rise with the size of territory held. Changes in the net benefit of territoriality due to relative stress levels of fish could influence territory size and even the decision of whether or not to attempt to hold territory. The importance of initial success in competitive interactions (Mason and Chapman 1965, Abbott et al. 1985) also justifies a bias towards territoriality. These results offer some explanation of why animals will spend apparently inordinate amounts of time and energy to gain dominance.

V. THE EFFECT OF FEEDING FREQUENCY ON AGGRESSIVE BEHAVIOUR

INTRODUCTION

Brown (1964) established the conditions under which a feeding territory should be defended: "If there is little to be gained by aggression and much to be lost then territorial behaviour will be selected against." Territories should be defended only when the gains (benefits) outweigh the losses (costs). This concept of economic defendability has formed the basis of theory predicting when a territory should be defended and what size it should be. A large body of evidence demonstrating the flexible space requirements of feeding territory holders, including juvenile salmonids, has since accumulated (reviewed by Dill 1978b), and several models that detail more specific facets of territoriality have been developed. A major contribution is that of Schoener (1971) who distinguished between foragers that attempt to maximize their rate of energy intake during foraging (Energy maximizers) and those that attempt to minimize the amount of time required to obtain a finite amount of energy (Time minimizers). Dill (1978b) considers juvenile coho salmon to be energy maximizers and McNicol and Noakes (1984) argue that juvenile brook charr are also energy maximizers.

A simple, primary prediction of this theory is that as energy maximizers juvenile salmonids that do not have full stomachs should increase their aggressiveness or territory size in response to a decrease in food availability. However, confirmation of this prediction has been surprisingly elusive. Dill (1978a) was able to demonstrate only an increased charge speed in a detailed investigation of several components of aggression, and Dill et al. (1981) showed an increased reactive distance at low food levels. The work of Slaney and Northcote (1974) and Mason (1976) best suggests a long term decrease in aggression if food availability increases under natural conditions. However, aggression has been found to increase (Newman 1956, Kalleberg 1958, Keenleyside and Yamamoto 1962, McNicol and Noakes 1984) or decrease (Symons 1968, Slaney and Northcote 1974) depending on the feeding ration, timing of feeding, measure of aggression or time of measurement. The general pattern of these results suggests a short term increase in aggression (possibly proportional to meal size) and a long term decrease in aggression in response to increased food availability. These contradictory responses are probably due to differing measures of aggression and food availability and discrepancies in parameters that have been altered with the intent of changing food availability.

If increased food availability results in decreased total aggression and aggressive peaks that are proportional to meal size, this suggests some consistent relationship between the peaks and valleys of the time course of aggression. How this time course responds to feeding has not been detailed and doing so is a major goal of this chapter.

In attempting to modify aggression by changing aspects of food presentation, investigators have used several definitions of food availability, none of which are known to be accepted by fish. Food availability for drift-feeding salmonids is best expressed as a rate involving a quantity per time or area. Previous research has involved time periods varying from 1 feeding/week (Keenleyside and Yamamoto 1962) to 1 feeding/15 min (Slaney and Northcote 1974). Depending on what time period fish use to assess food availability, infrequent feedings could be perceived as long periods of starvation. Thus when investigators have altered ration, feeding interval can be a confounding variable. Regular, infrequent feeding regimes are unlikely to resemble the availability of food in the wild, where irregular or clumped availability may be expected. Dill (1978a) and McNicol and Noakes (1984) have both identified the fish's assessment time period as crucial information for further work.

In addition to the uncertainty of the time period used by fish to assess their food supply, the sensory mechanism by which fish assess the available food is unknown. Possibilities include memory of past feeding activity over time, gut fullness or physiological measures such as blood parameters (Teitelbaum 1966).

This study attempted to assess the time period and mechanism of assessment by feeding a constant daily ration of food and varying the frequency of feeding. If the frequency of feeding activity is used to assess food availability, then total daily aggression should vary with the frequency of feeding bouts. If some other mechanism monitors food availability over longer periods (i.e., one day) total daily aggression should remain constant under constant daily rations. This does not exclude the possibility that fish also monitor short-term food availability. However, fine-scale measurement of the time course of aggression following feeding should show these other trends.

Behaviour under different feeding regimes was examined concurrently with the growth experiments of Chapter III. The random and 1-h (X 24h) feeding regime were included as possibly being more similar to availability patterns in the natural environment in certain aspects. Intensive behavioural sampling was conducted to determine the exact time course of aggression following feeding.

METHODS

All fish groups, treatments, and environmental variables are as described in Chapter III. On the fifth day of feeding, black and white videotape recordings were made. A large sheet of white plastic was suspended in front of the tanks on the morning of day 1, and appropriately spaced holes were cut to allow filming without disturbing the fish.

Growth Trials 1 & 2:

In these trials only one camera mounted on a tripod was available. By raising and lowering the camera a vertical pair of tanks were filmed for one minute each and the tripod was moved laterally to film the next pair of tanks. Movement between tanks required 15 to 30 s. Samples were not evenly distributed over time, but were clustered about feeding periods as activity changed most quickly at this time. During the middle of the day when no feedings occurred and the fish were relatively inactive, several 2-min samples were taken for each tank. Thus, each point in a time course of aggression for a feeding regime represents the average of five tanks over a 12.5 to 15-min period in the case of 1-min samples, and over a 22.5 to 25-min period in the less frequent case of 2-min samples.

Growth Trial 3:

A third bank of tanks was added for this trial. Shelves were built on a wheeled cart to support the video camera at the height of the banks of tanks. The camera was moved to each shelf to film all tanks in a vertical row for 30 s each and then the apparatus was wheeled laterally to cover the next vertical row. Movement between tanks required approximately 5 to 10 s. Thus each point in a time course of aggression represents the average of 5 tanks over approximately 9 min.

Growth Trials 4 & 5:

In these trials three cameras were obtained and placed on each shelf of the camera stand. All three tanks in a vertical row could then be filmed and lateral movement required approximately 5-10 s. Each sample therefore required approximately 3 min to obtain. Tanks were sampled within the 5-min period before each feeding and the 5-min period after feeding and at the mid-point between feeds. The randomly fed tanks were sampled on the same regime as the regular half hour regime. Results from one tank in each regime in growth trial 5 were excluded due to high mortality.

Behaviour Analysis:

Videotapes were viewed and behavioural events recorded on a Datamyte 800 event recorder. Each sample was viewed several times with the use of slow motion and stop-action to obtain the following measures:

1. The number of fish performing aggressive acts;

2. The number of fish receiving aggressive acts;
3. The percent of total sample time in which aggressive acts occurred.

The following aggressive behaviours were recorded:

1. Nip - either visible or probable jaw contact;
2. Charge - a very fast approach of greater than 1 body length (if less than one body length it was usually included as a nip);
3. Approach - a slow movement directed towards another fish;
4. Chase - a high speed continuation of a charge or approach and in which the recipient flees.

Due to high variation in average daily aggression between tanks within a feeding regime, for presentation of time course data, each tank score was normalised to the daily tank mean. These scores were then averaged.

RESULTS

General observations:

All groups were observed feeding on the first day following weighing. Usually a dominant fish was stationed in the upper central portion of the tank and subordinates held about the edges and corners of the tank. When more than one fish was acting in an aggressive fashion (this tended to occur after feeding) the tank appeared to be divided vertically with the alpha fish above. Thus, it appeared as if the dominate fish were maintaining territories.

Subordinate fish sometimes swam under the mesh on the bottom of the tank. This caused a certain amount of disturbance as the mesh had to be lifted to retrieve the fish. The fish involved were usually small relative to the tank average and, by their colour and behaviour, often appeared to be stressed.

Although fish in all tanks were observed to feed on the first day of the experiment, the tanks containing the smallest and largest fish of each feeding regime did not appear to adapt to the experimental regime readily; fewer fish were observed to feed and they exhibited more symptoms of stress such as a rapid gill ventilation and fin beat and dark colouration. Fish did not appear to change their behaviour in response to observed activity, or the brighter lights used during filming. However, fish were observed to respond to the sound of the fish feeder motor when other tanks were fed.

Total daily behaviour:

There were few differences between regularly fed regimes in their daily aggression measured as: aggressive acts per fish per 30 s, per cent time engaged in aggression, nips per fish per 30 s, charges per fish per 30 s, chases per fish per 30 s, approaches per fish per 30 s, average number of aggressors (Figs. 9-15; p values are given in the figure legends). No consistent trend is apparent. Values for aggression rates in growth trial 5 were most frequently different from (higher than) those associated with regular feedings.

Time courses:

In all feeding regimes (Figs. 16-28) there was a significant increase in the number of aggressive acts following a feeding. In 74 of 113 observed feedings the number of aggressive acts at the sampling point immediately post-feeding was higher than in the immediate pre-feeding sample (sign test, p=0.019, Table 7). Considering individual feeding regimes only the 0.5-h interval and the 1-h interval (over 24 h) did not show increases in the number of aggressive acts following feeding. The 2-, 4- and 24-h interval feedings showed peaks after all feeds. The small sample sizes for regimes that had 4 or less feedings per day make statistical tests meaningless, but the coincidence between aggressive peaks and feeding times is obvious (Figs. 16 to 21). Per cent time engaged in aggression increased following 73 of 113 feedings (sign test, p=0.019), but intensity, measured as the ratio of nips to all acts, did not increase significantly following feeding (sign test, p=0.425). The number of aggressors increased following feeding 75 times in 113 observed feedings (sign test, p=0.019). When feedings are infrequent, low scores immediately prior to feeding were recorded (i.e., Figs. 16, 17, and 18). This did not concur with subjective impressions of the observers (J.C.A and R. Hotson); on a finer scale it appeared that aggression and overall activity increased prior to feeding time. Daily and twice daily feeding regimes were also characterised by high levels of aggression just after the lights came on in the morning and just before they went off in the evening (Figs. 16 to 20). Some of the figures indicate that the sound of fish feeders operating over adjacent rows of tanks may have initiated aggression, as small peaks at these time are observed (Figs. 21-22).

The average height of peaks of aggressive acts following feeding, measured from the sample immediately before feeding to the point where the sign of the slope first becomes negative, showed a non-significant trend (ANOVA, p=0.171) of decreasing peak height with increasing frequency of feeding (Fig. 29).

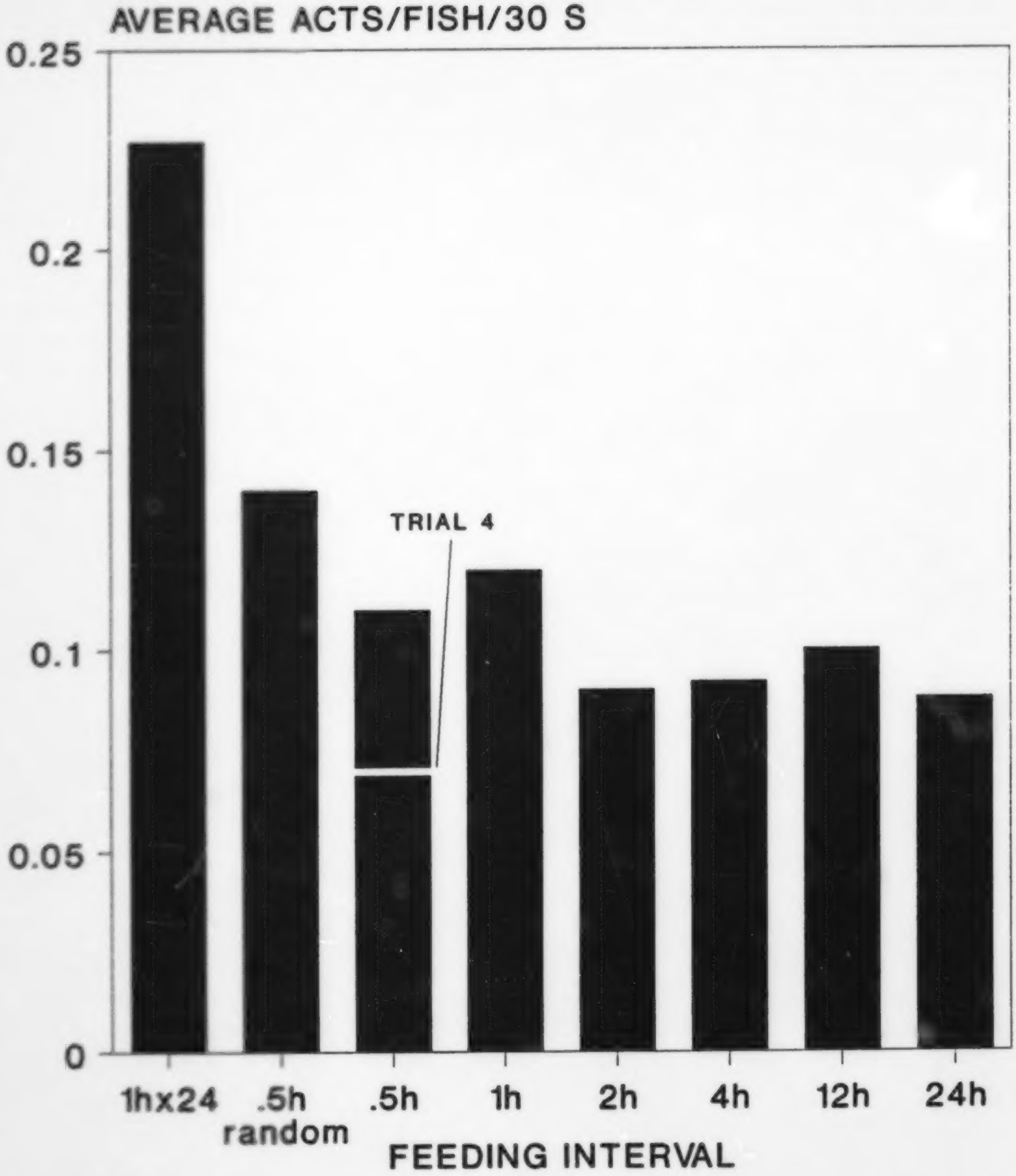

Figure 9. Frequency of aggressive acts of eight juvenile steelhead under various feeding regimes. (1hX24h & 4h, & 24h different at the .05 level, ANOVA, Dunn -Sidak a posteriori method). N as in Fig. 3. Vertical lines represent standard errors. The white bar at 0.5 h represents the value for trial 4 alone.

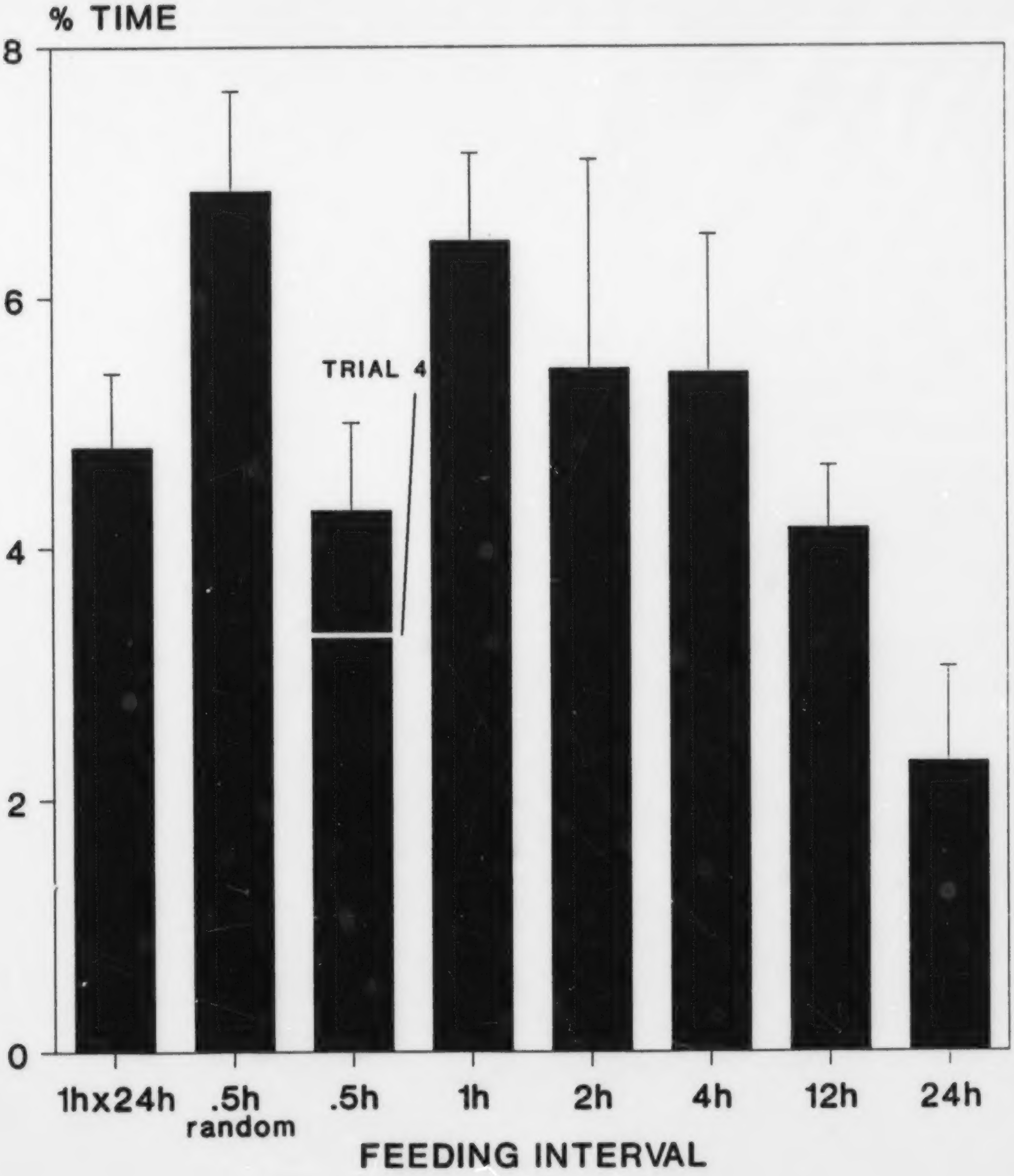

Figure 10. Per cent time engaged in aggression by groups of eight juvenile steelhead under various feeding regimes. (24h & 12h, 4h, 2h, 1h, & 1h(X24hr) different at the .05 level, ANOVA, Dunn-Sidak method). N as in Fig. 3. Vertical lines represent standard errors.

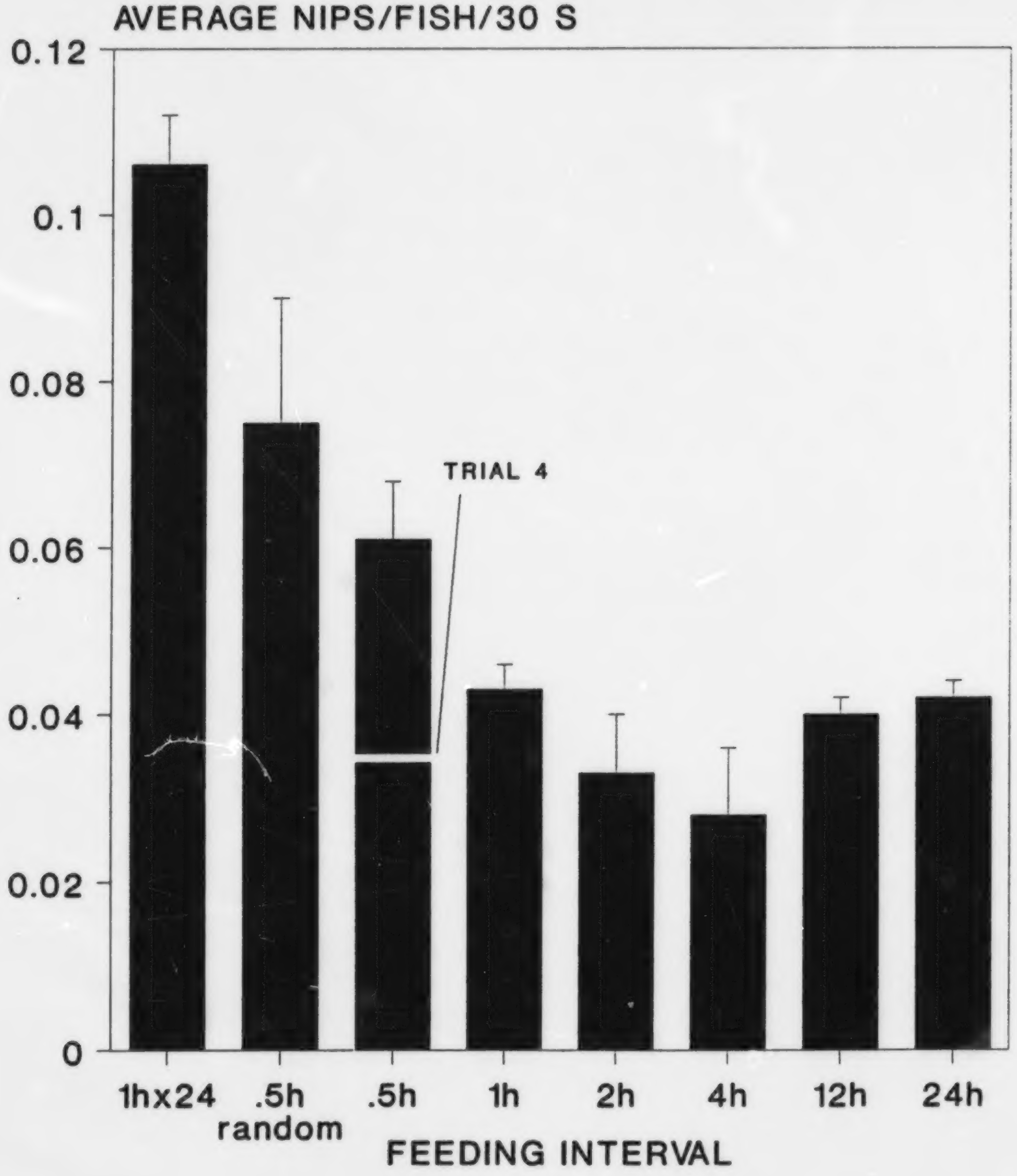

Figure 11. Frequency of nips in groups of juvenile steelhead. (1h(x24h) & 1h, 2h, 12h, & 24h; .5h & 4h; random & 24h different at the .05 level, ANOVA, Dunn-Sidak method). N as in Fig. 3. Vertical lines represent standard errors.

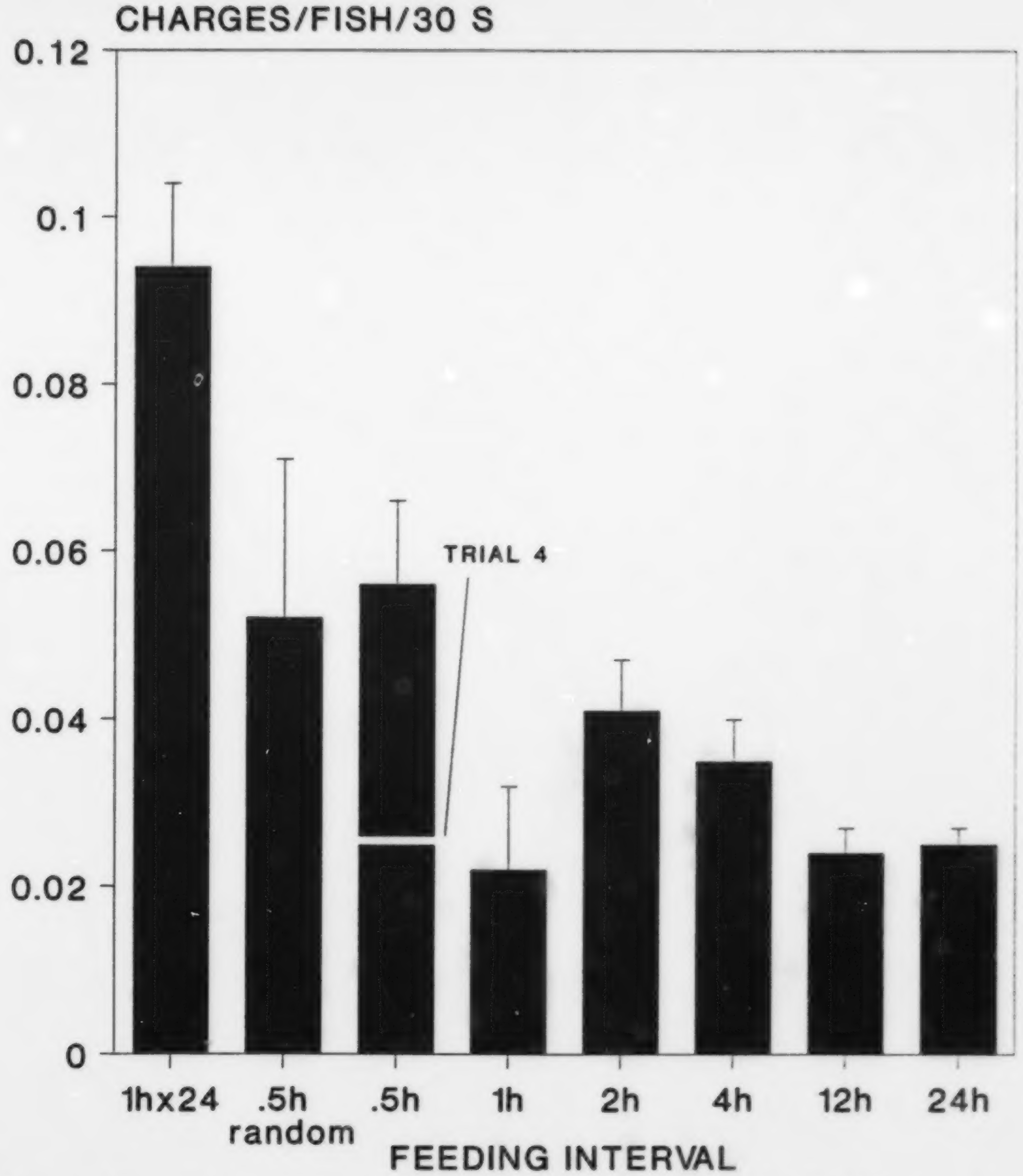

Figure 12. Frequency of charges in groups of juvenile steelhead. (1h(X24h) & 1h, 2h, 4h, 12h, & 24h different at the .05 level, ANOVA, Dunn-Sidak method). N as in Fig. 3. Vertical lines represents standard errors.

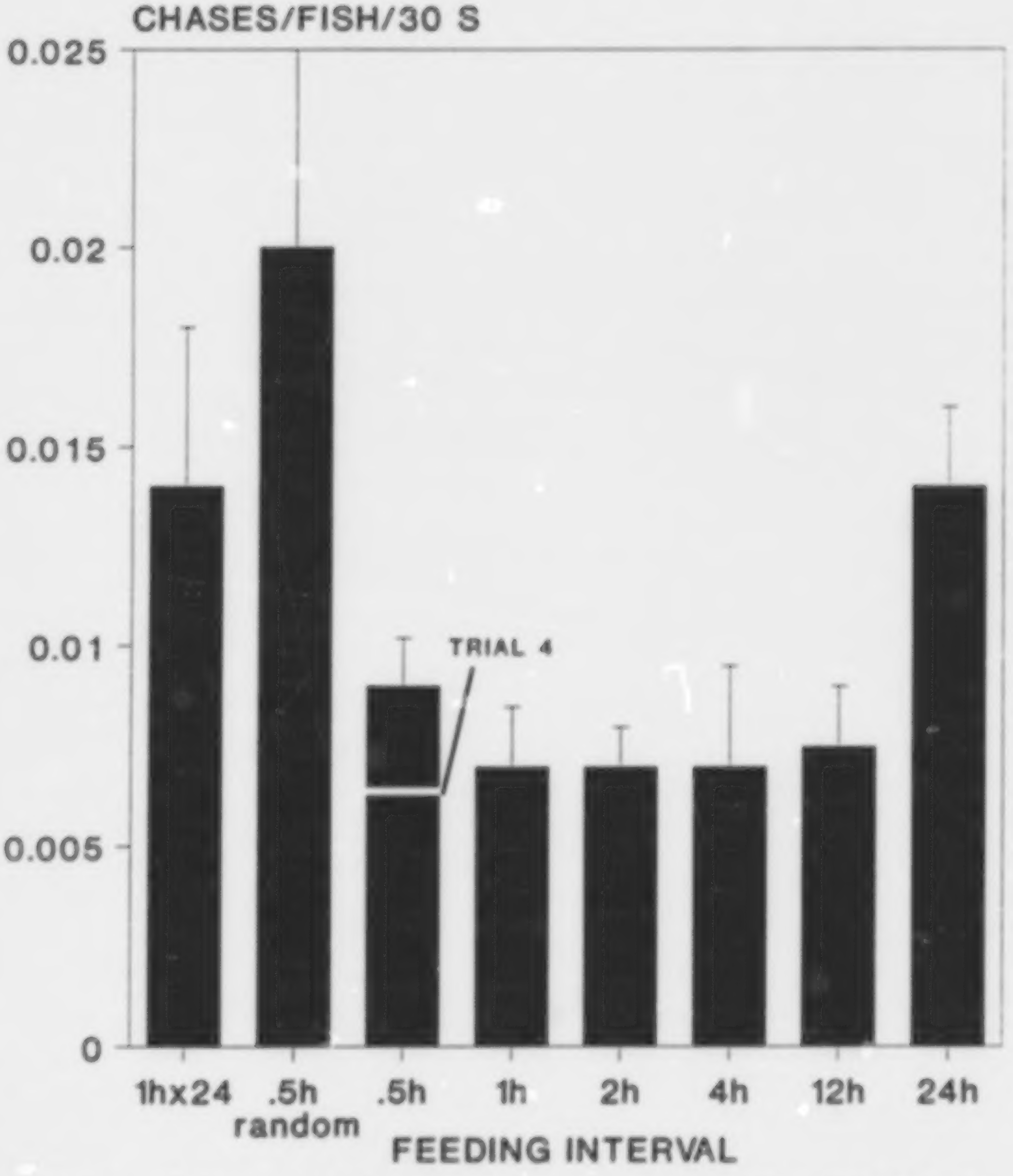

Figure 13. Frequency of chases in groups of eight steelhead. (No significant difference at the .05 level, ANOVA, Dunn-Sidak method). N as in Fig. 3. Vertical lines represent standard errors.

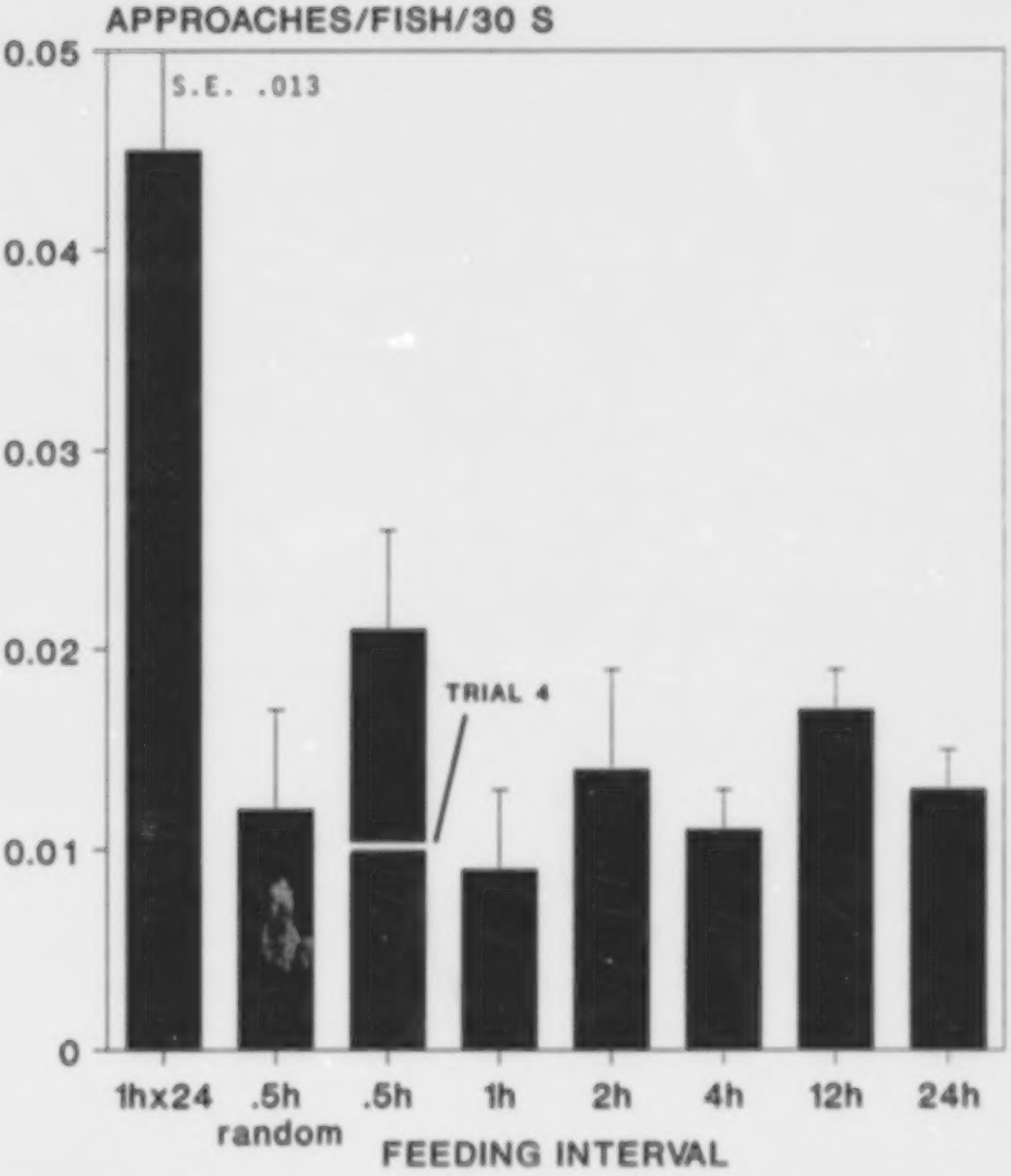

Figure 14. Frequency of approaches in groups of eight steelhead. (Random, 1h(X24h) & .5h all different from all other regimes at the .05 level, ANOVA, Dunn-Sidak method). N as in Fig. 3. Vertical lines represent standard errors.

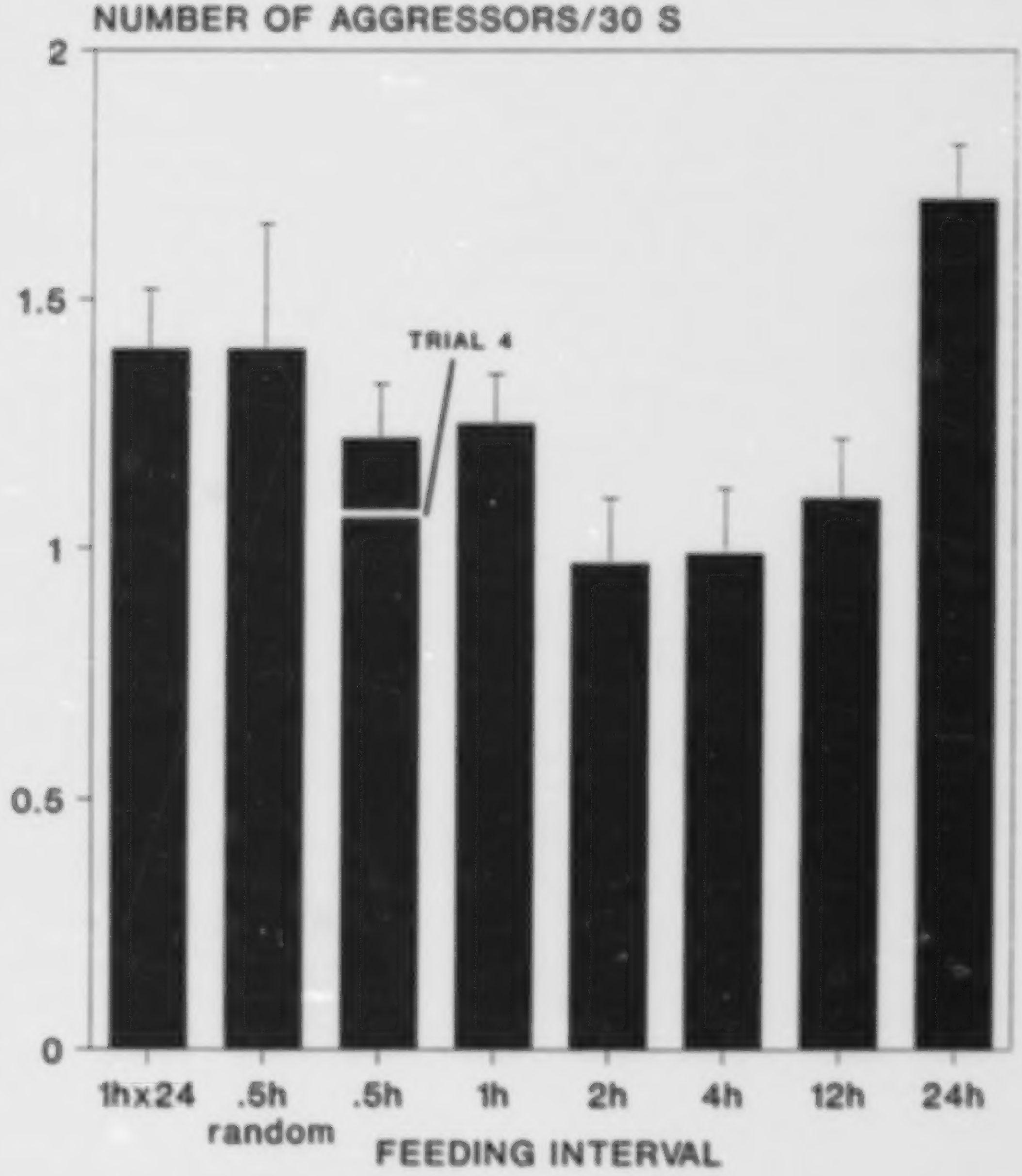

Figure 15. Average number of aggressors observed per 30 s in groups of eight steelhead. (24h & 12h, 4h & 2h different at the .05 level, ANOVA, Dunn-Sidak method). N as in Fig. 3. Vertical lines represent standard errors.

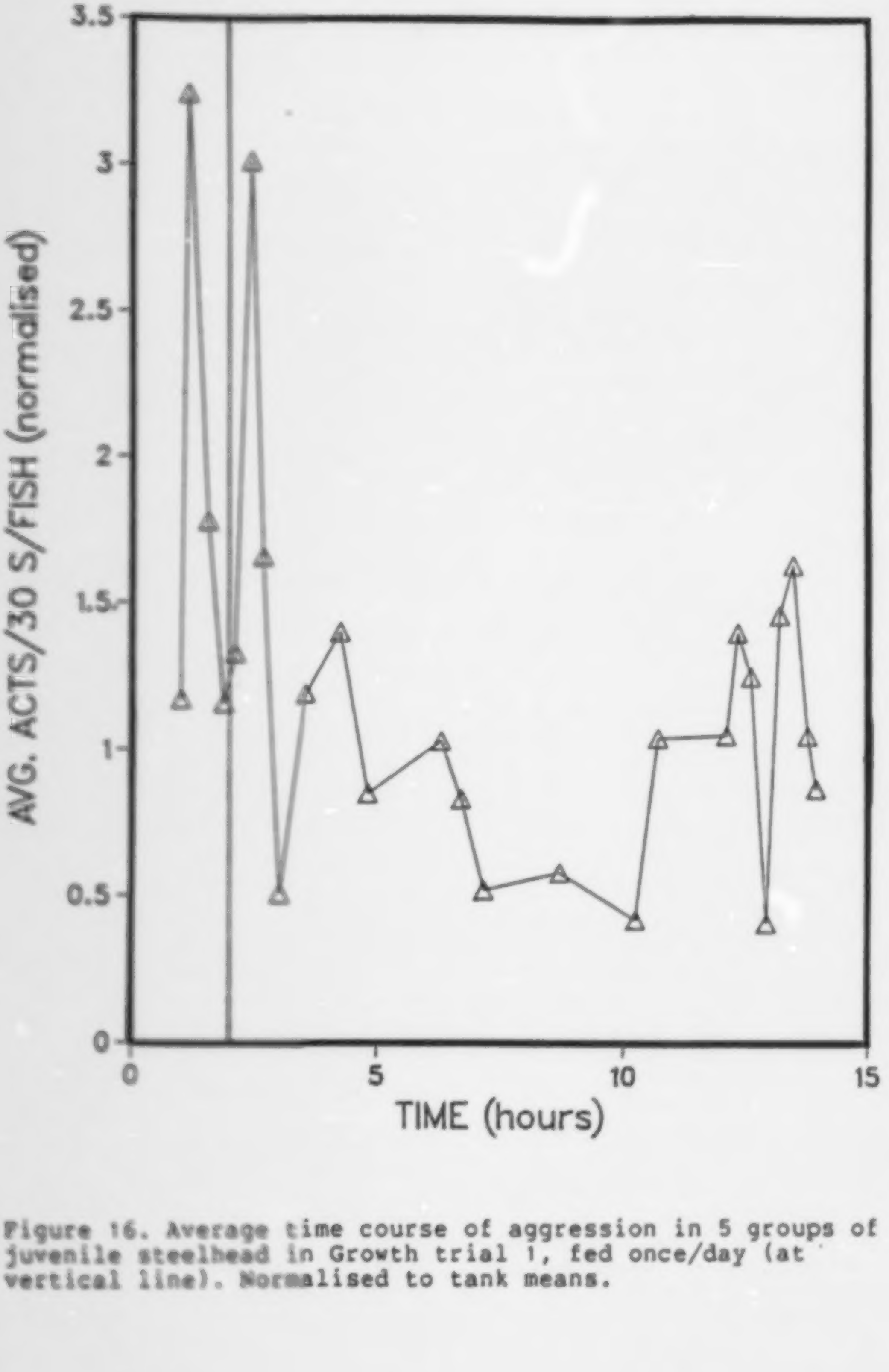

Figure 16. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 1, fed once/day (at vertical line). Normalised to tank means.

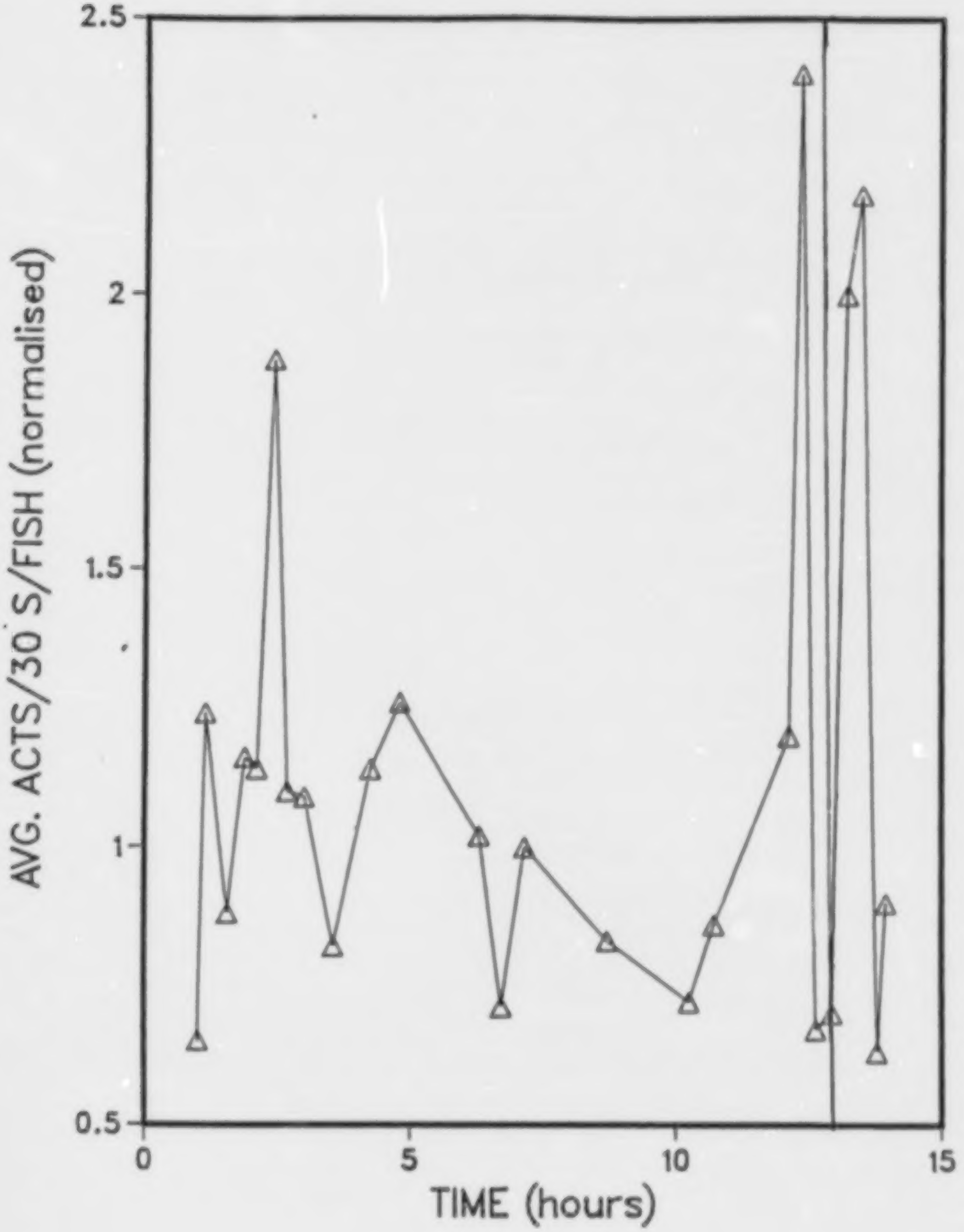

Figure 17. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 1, fed once/day (at vertical line). Normalised to tank means.

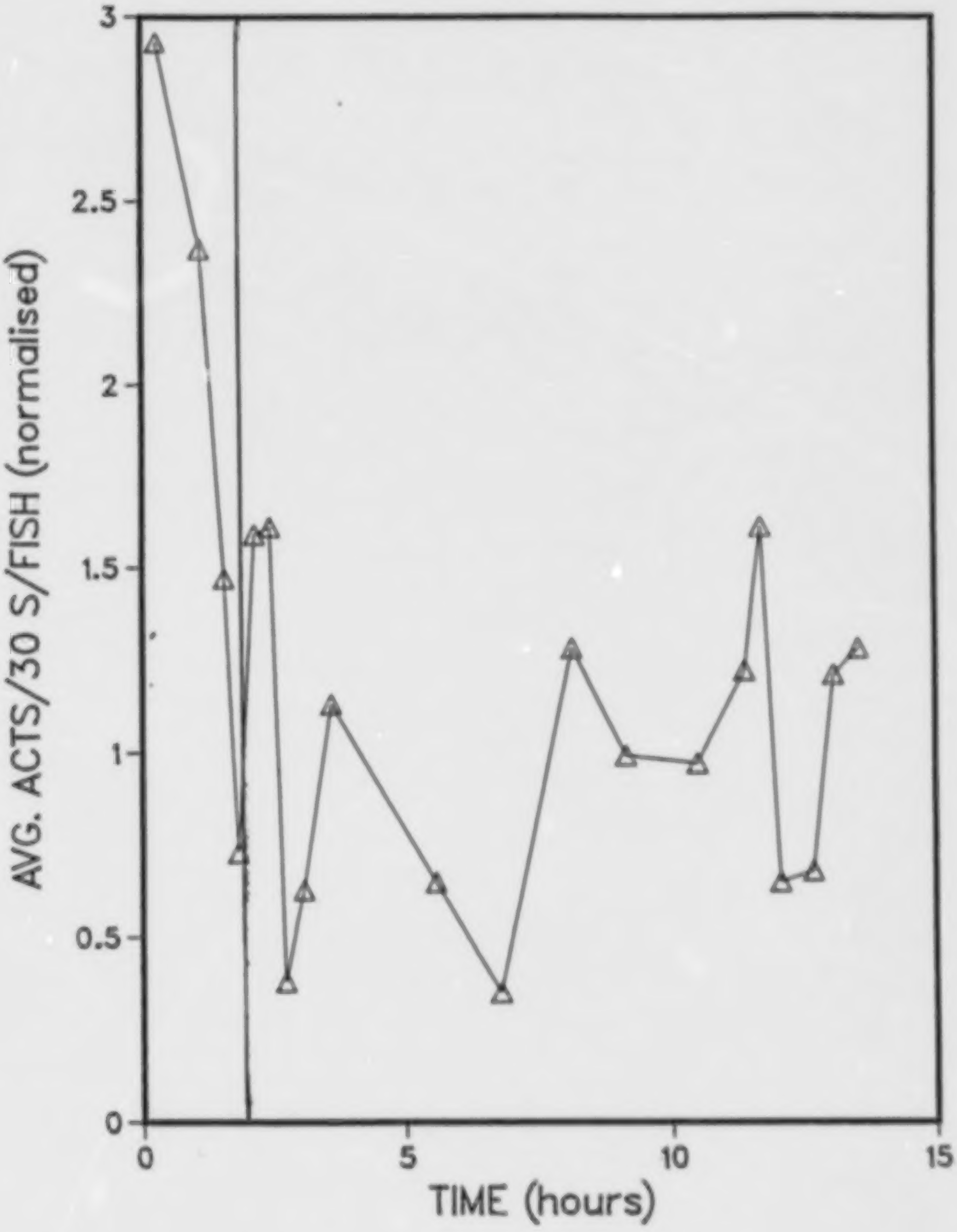

Figure 18. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 2, fed once/day (at vertical line). Normalised to tank means.

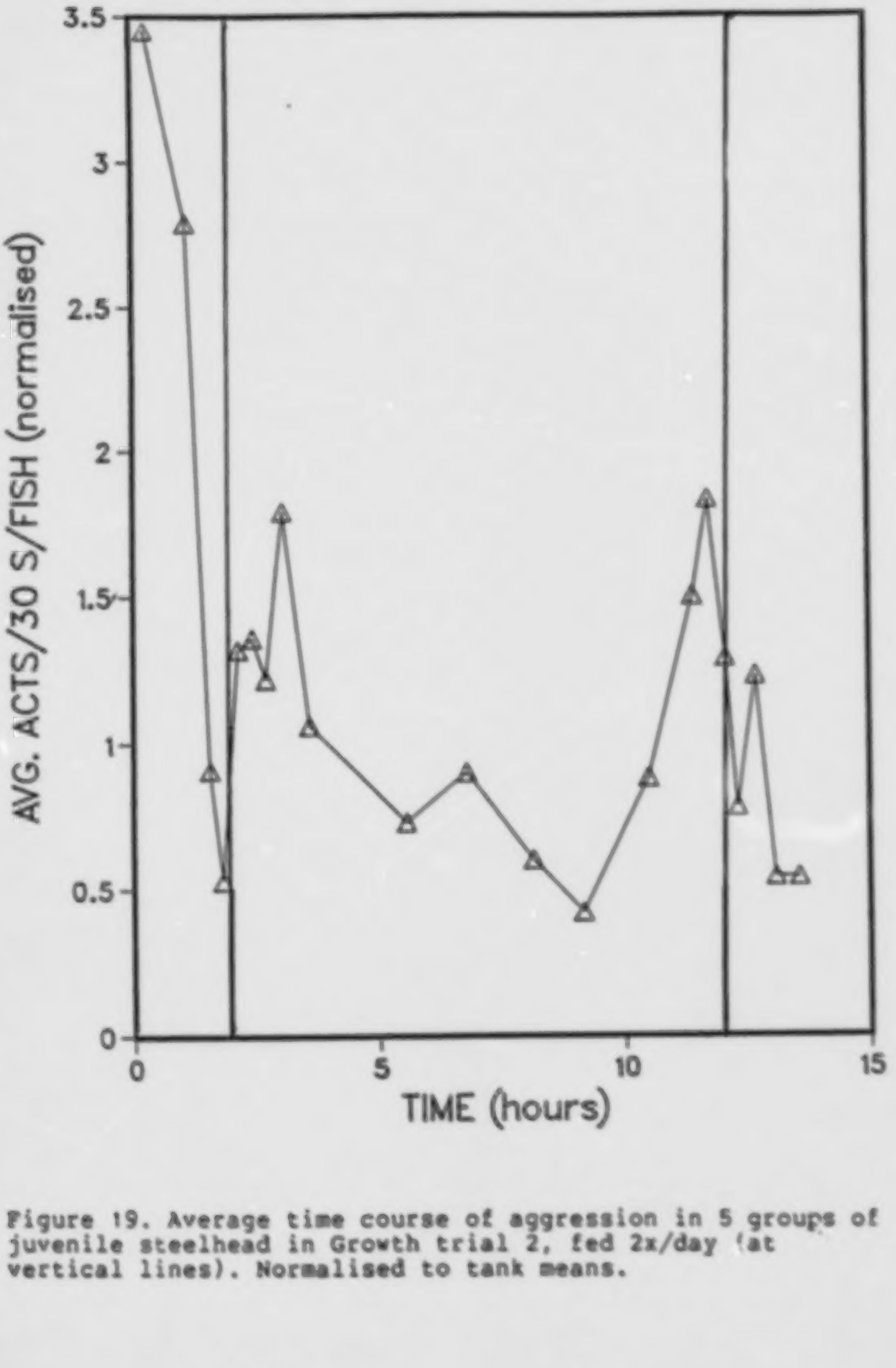

Figure 19. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 2, fed 2x/day (at vertical lines). Normalised to tank means.

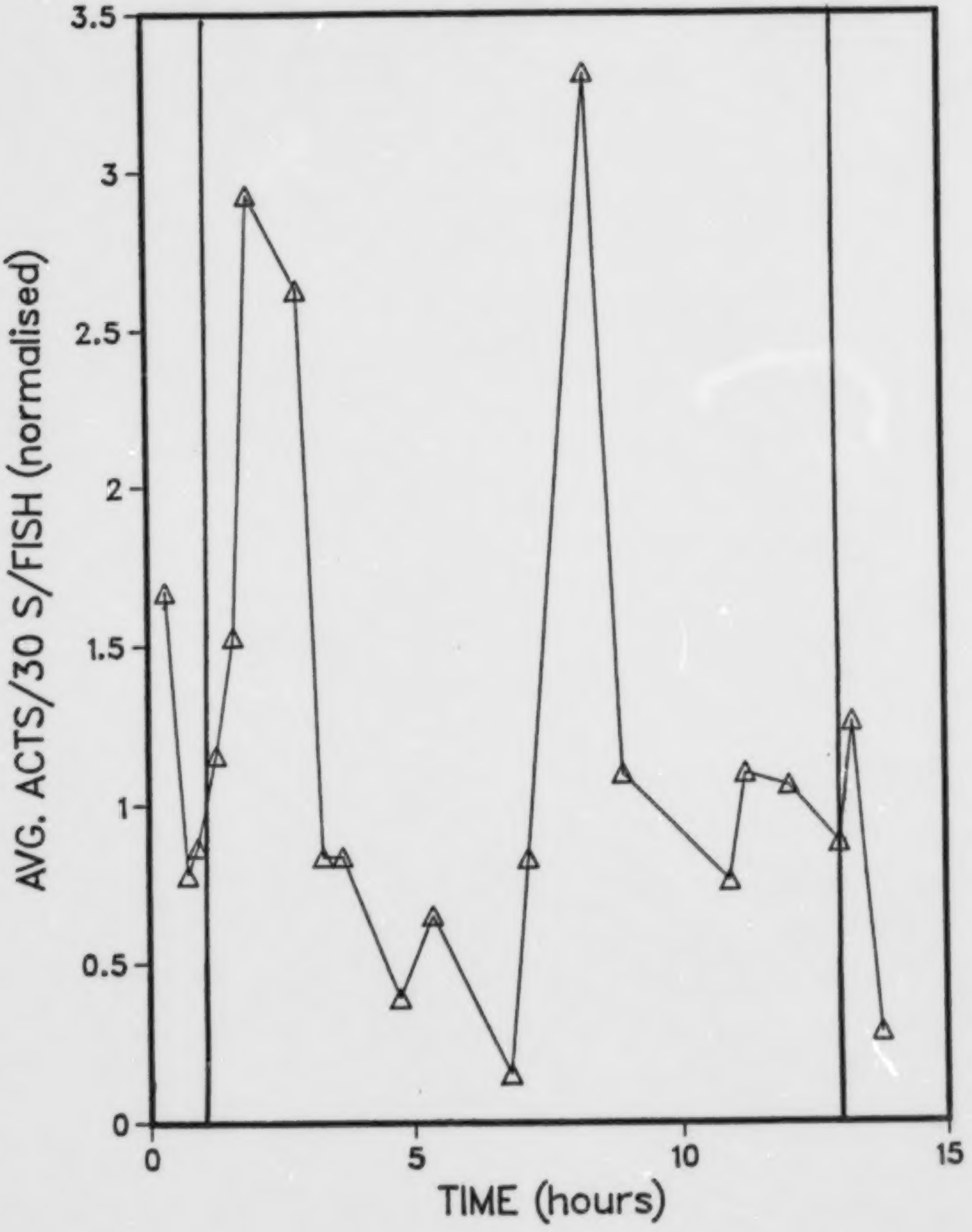

Figure 20. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 3, fed 2x/day (at vertical lines). Normalised to tank means.

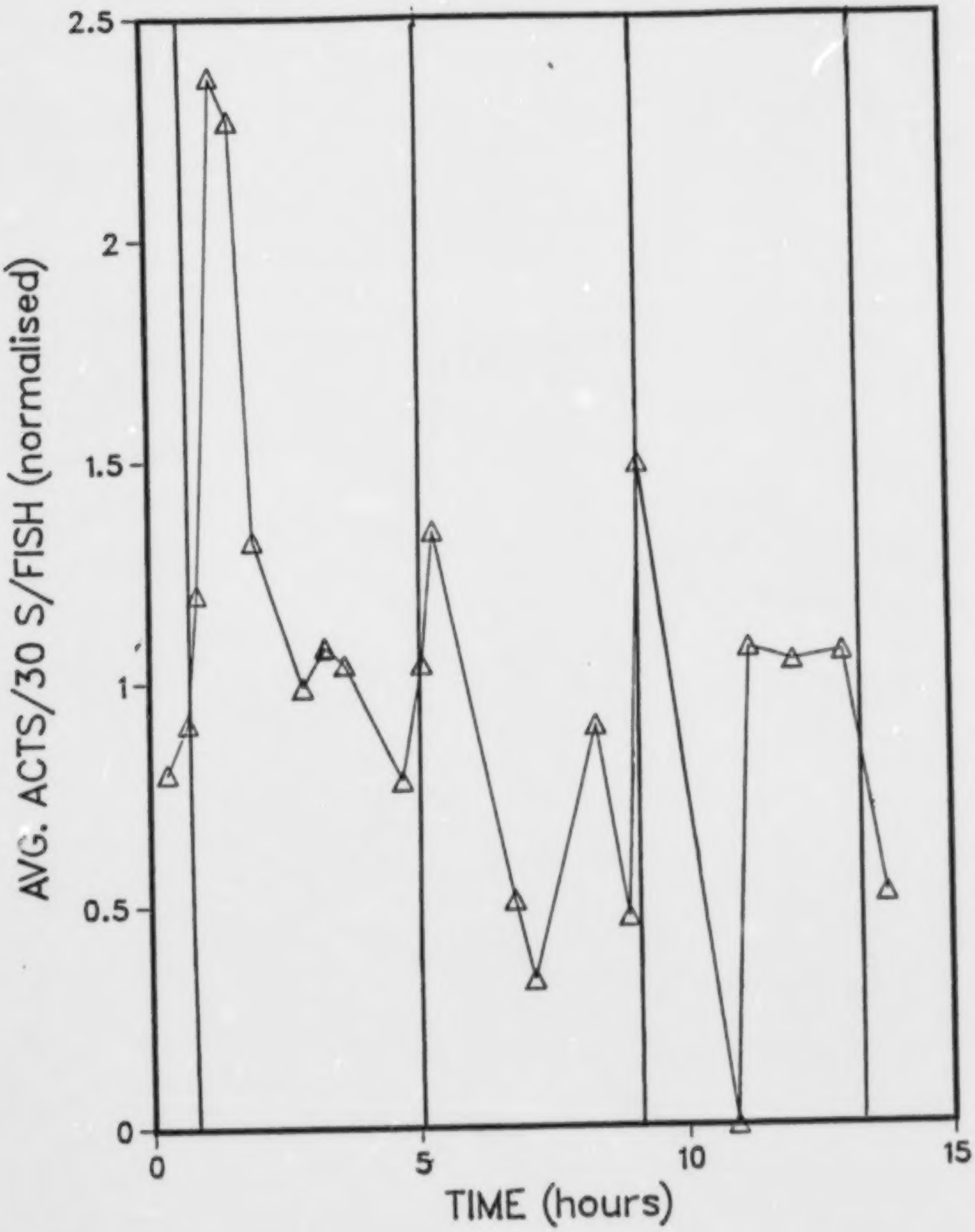

Figure 21. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 3, fed at 4-h intervals (at vertical lines). Normalised to tank means.

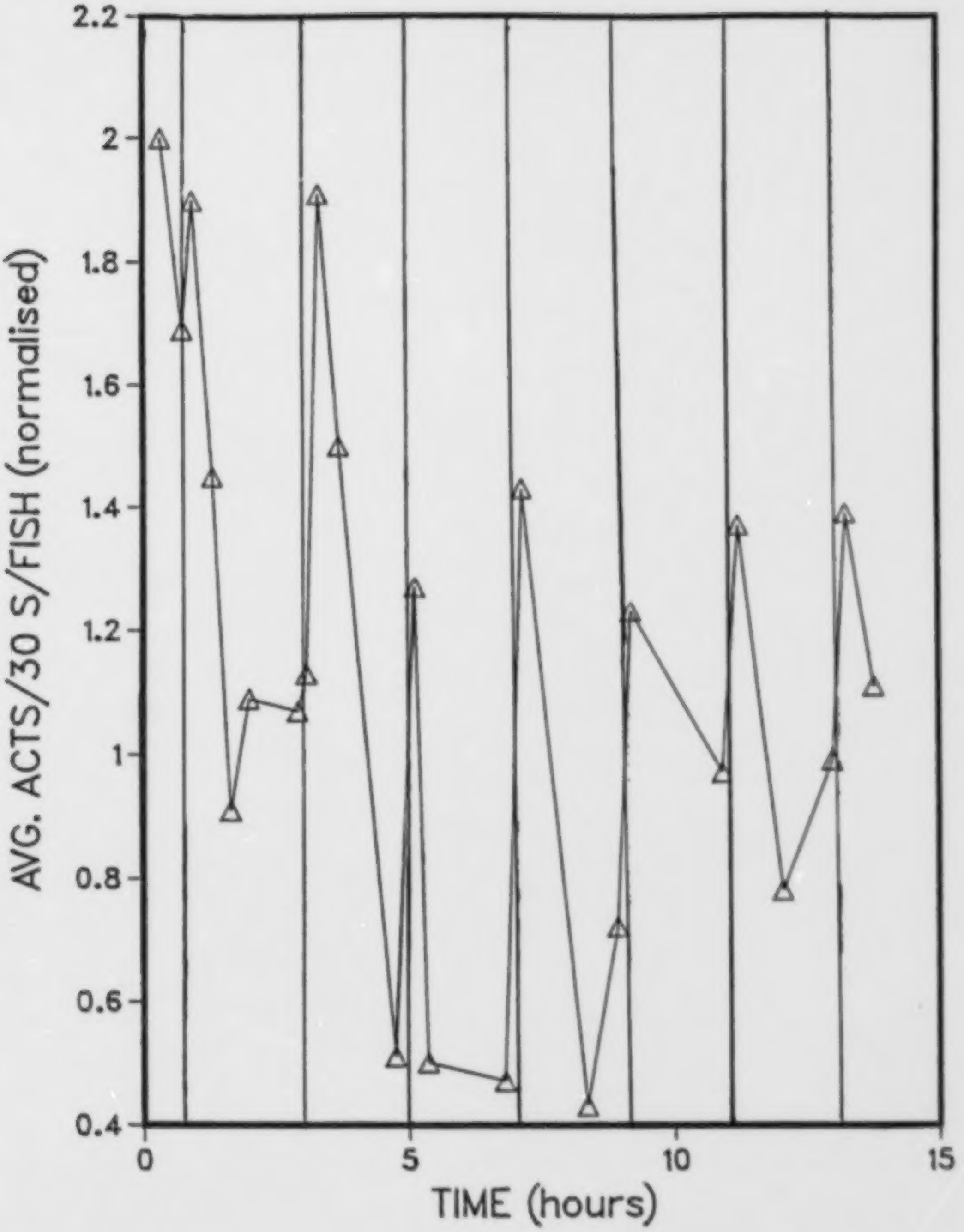

Figure 22. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 3, fed at 2-h intervals (at vertical lines). Normalised to tank means.

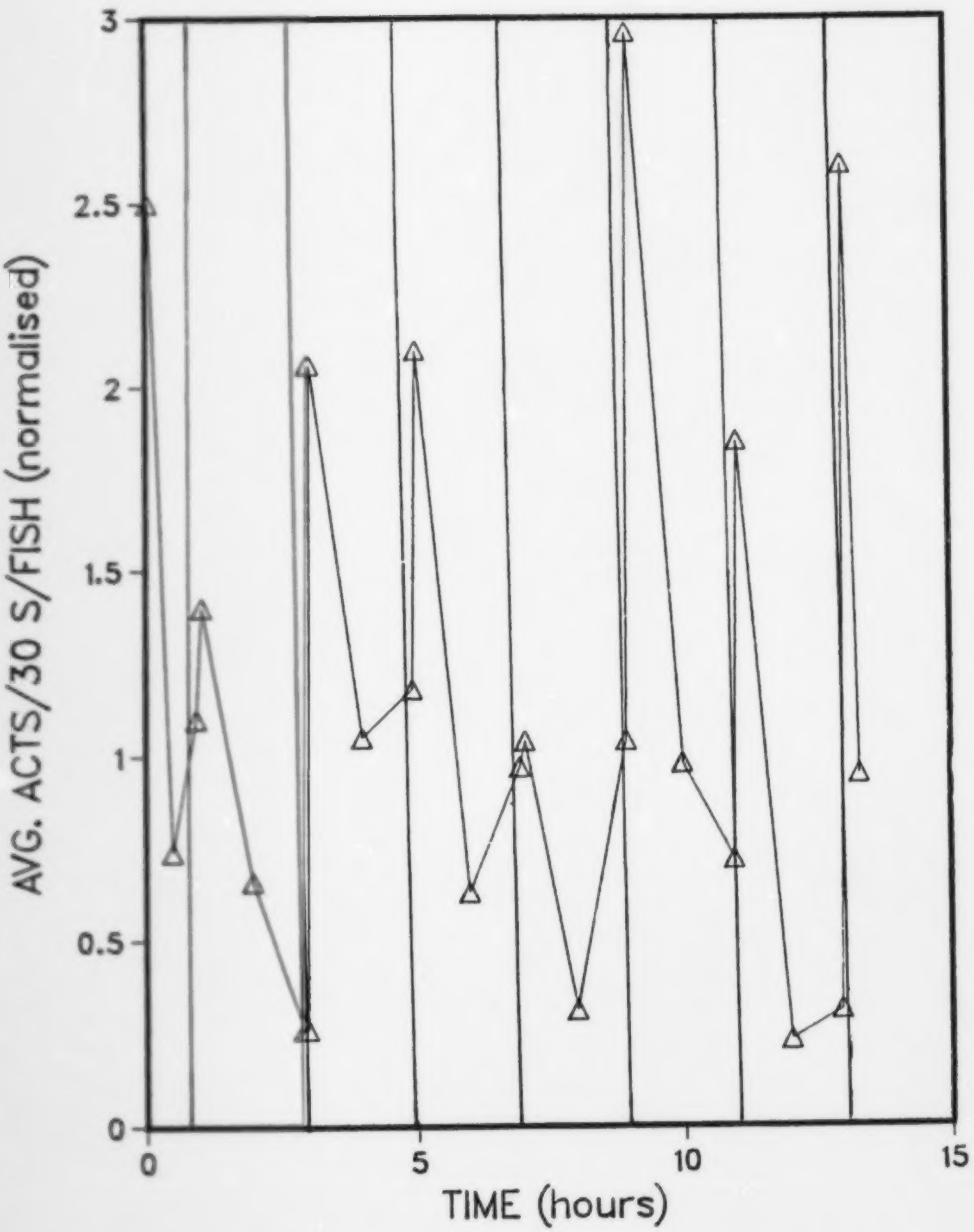

Figure 23. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 4, fed at 2-h intervals (at vertical lines). Normalised to tank means.

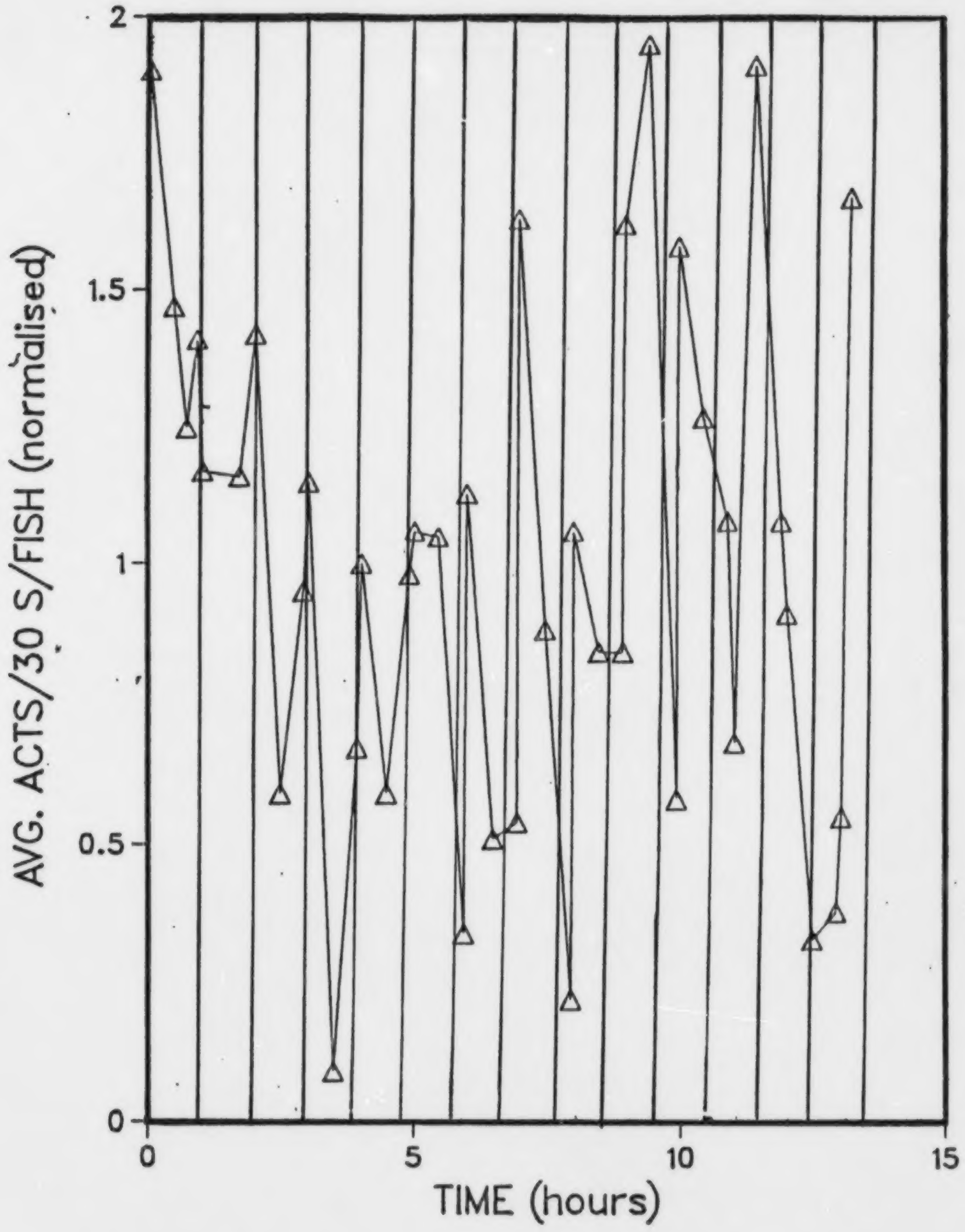

Figure 24. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 4, fed at 1-h intervals (at vertical lines on overlay). Normalised to tank means.

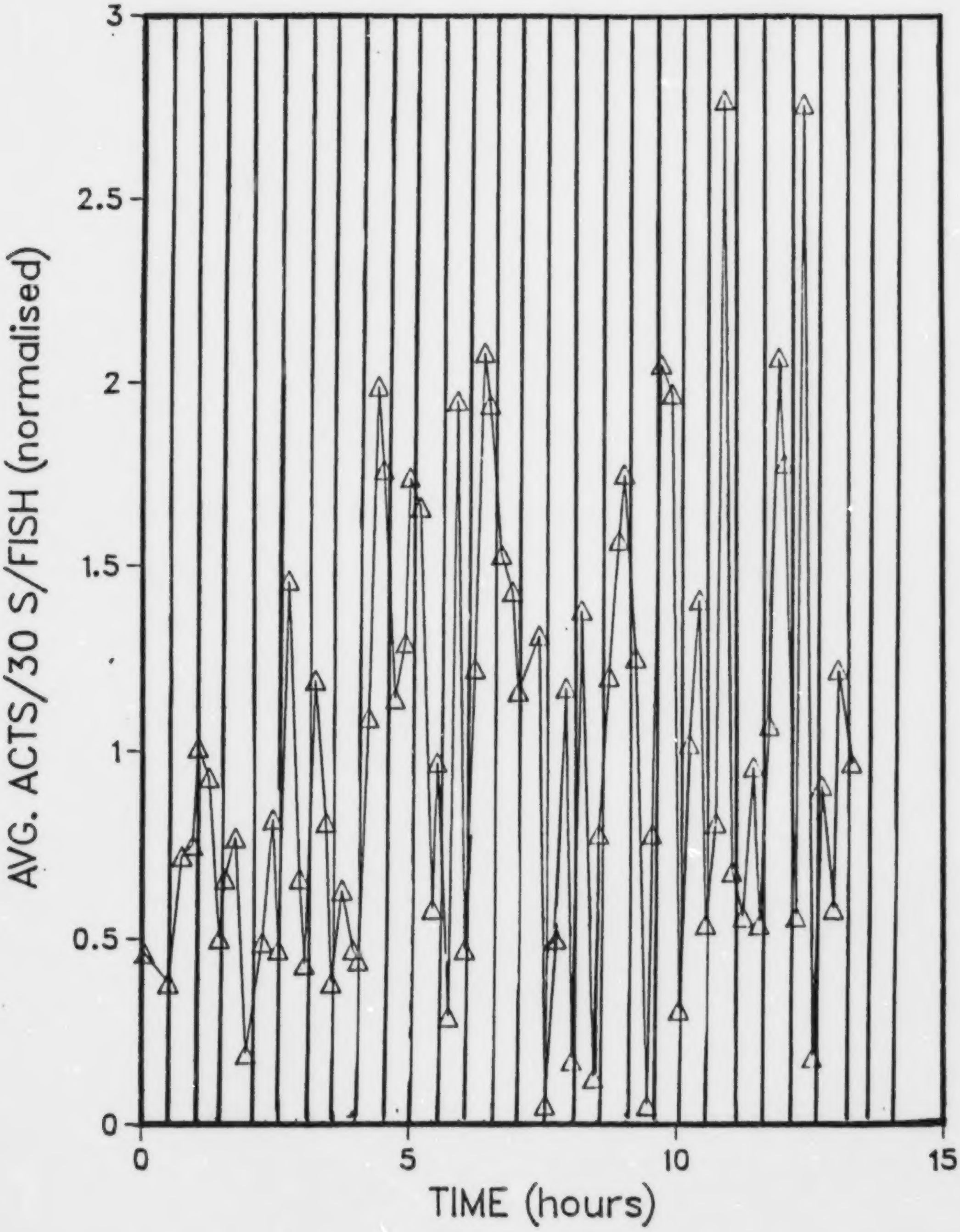

Figure 25. Average time course of aggression in 5 groups of juvenile steelhead in Growth trial 4, fed at 0.5-h intervals (at vertical lines on overlay). Normalised to tank means.

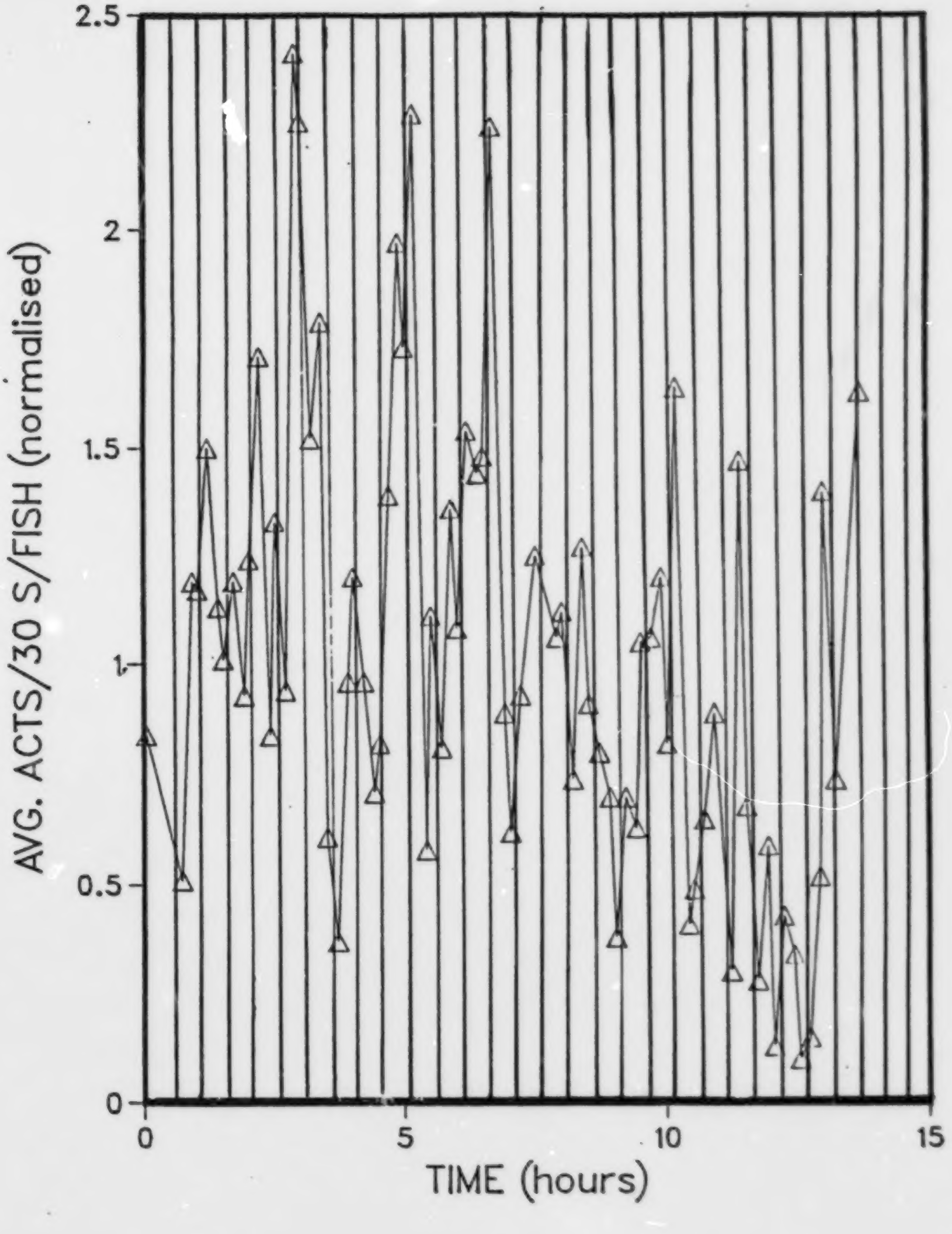

Figure 26. Average time course of aggression in 4 groups of juvenile steelhead in Growth trial 5, fed at 0.5-h intervals (at vertical lines on overlay). Normalised to tank means.

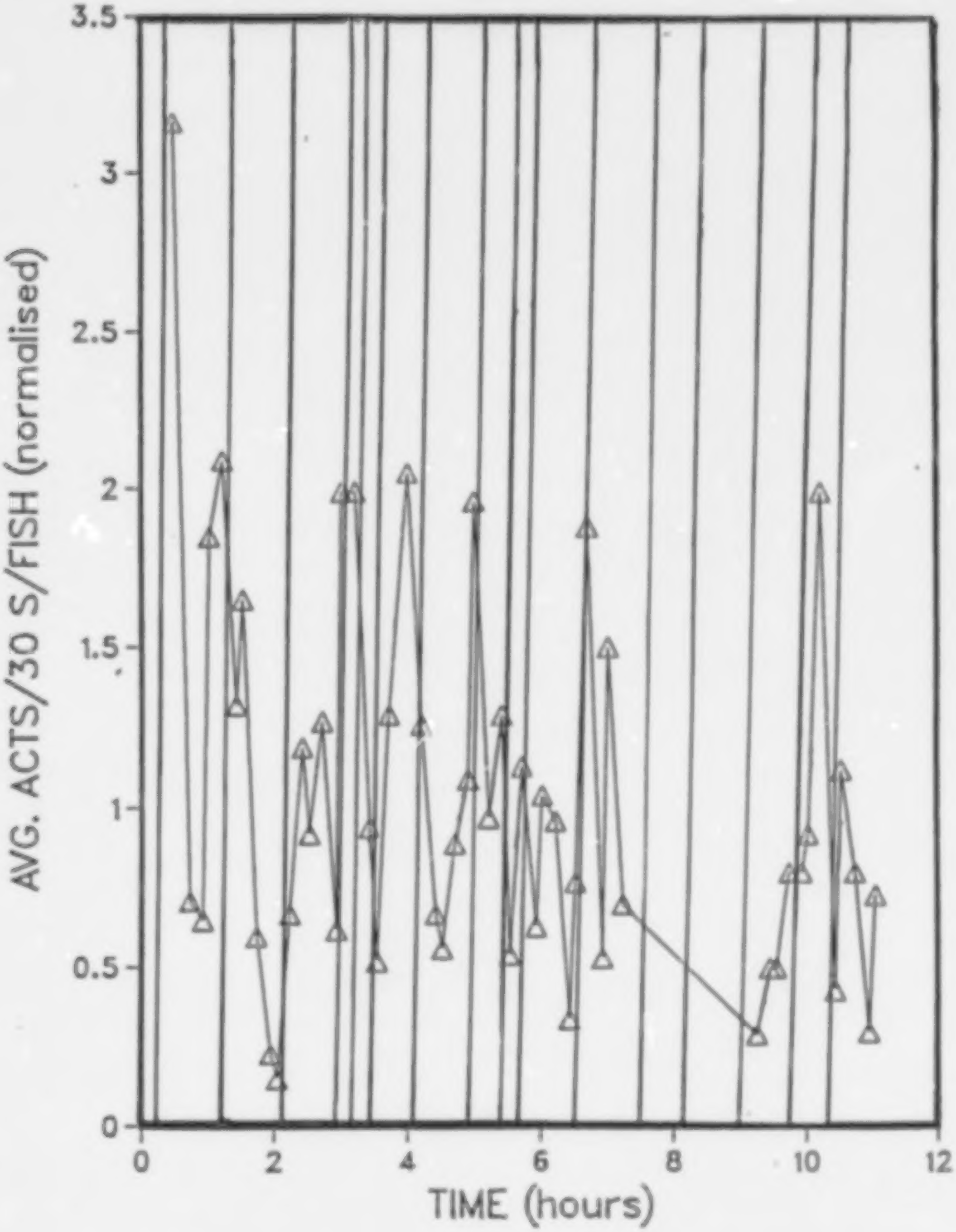

Figure 27. Average time course of aggression in 4 groups of juvenile steelhead in Growth trial 5, fed randomly at vertical lines on the overlay (0.5-h average interval). Normalised to tank means.

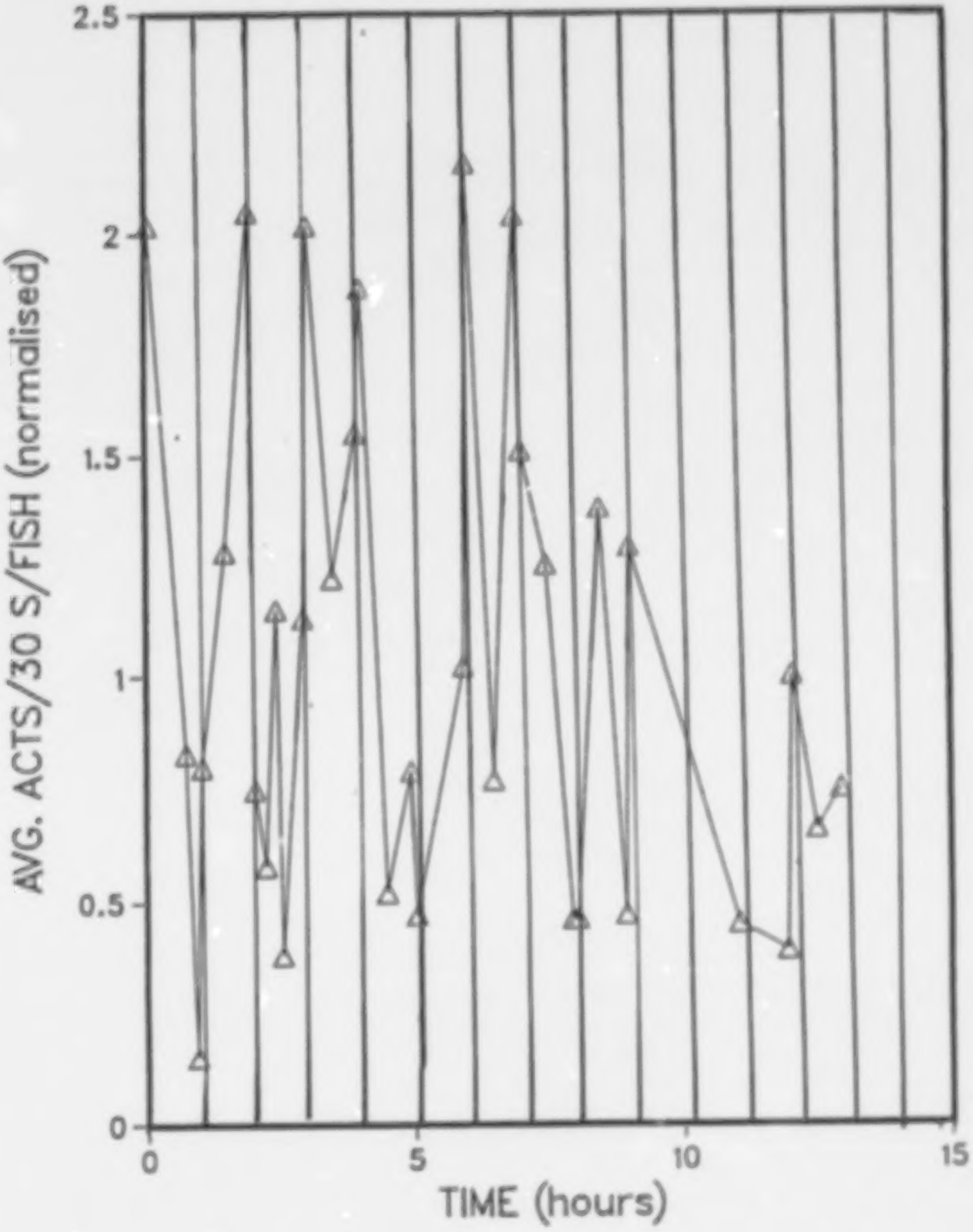

Figure 28. Average time course of aggression in 4 groups of juvenile steelhead in Growth trial 5, fed 1x/h(x24 h) (at vertical lines on overlay). Normalised to tank means.

Table 7. The frequency of increase of various measures of aggression following feeding under different feeding regimes (occurrence of increase/total feedings observed). P values from sign test in parentheses.

Feeding Interval	Acts	% Time	Nips/Acts	# of Aggressors
24hr	3/3(.125)	3/3(.125)	2/3(.25)	3/3(.125)
12hr	3/4(.25)	3/4(.25)	3/4(.25)	3/4(.25)
4hr	4/4(.062)	3/4(.25)	2/4(.375)	4/4(.062)
2hr	14/14(.001)	11/14(.022)	9/14(.122)	11/14(.022)
1hr	11/13(.01)	9/13(.022)	6/13(.209)	9/13(.022)
.5hr	21/50(.102)	27/50(.16)	20/50(.102)	28/50(.16)
Random	11/13(.01)	10/13(.035)	9/13(.087)	11/13(.01)
24hr (1/hr)	7/12(.193)	7/12(.193)	6/12(.226)	6/12(.226)
Overall	74/113(.019)	73/113(.019)	57/113(.425)	75/113(.019)

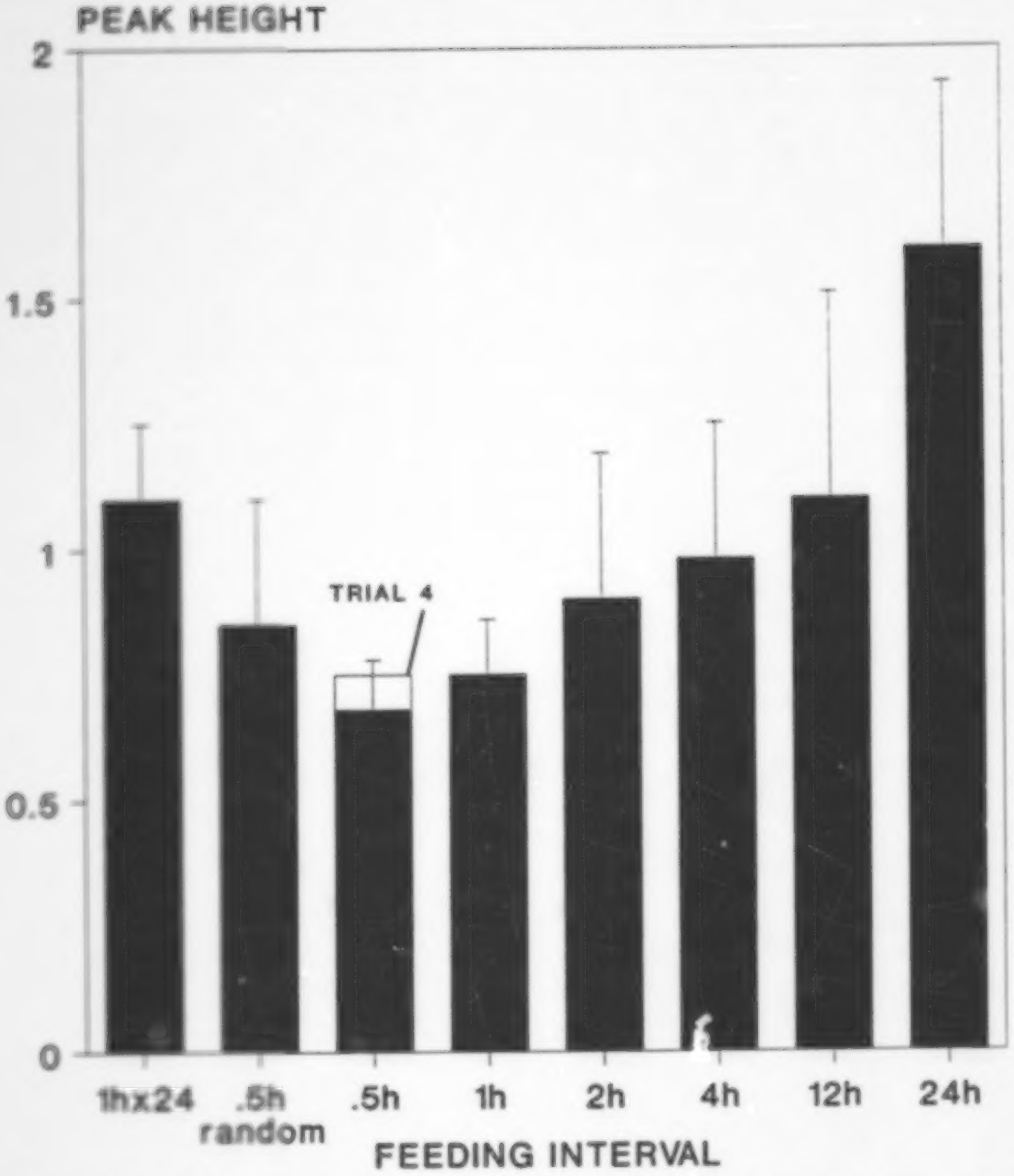

Figure 29. The height of peaks of aggression (normalised units) in groups of steelhead under various feeding regimes. Units as in Figs. 16-28. The open bar at .05 h represents the value of trial 4 alone.

DISCUSSION

There were few differences in total daily aggression attributed to feeding regime as measured by a variety of aggressive indices. When differences occurred they most frequently involved random and 24-h schedules. Within a day there were marked variations in levels of aggression. Peaks were temporally associated with feeding, and the size of the peaks, measured by the number of aggressive acts, tended to decrease as the frequency of feeding increased and the amount of food present at each feeding decreased.

That total daily aggression is constant when daily ration is constant does not contradict a hypothesis that aggressive levels are based on an assessment of daily ration. That fish did not alter their total levels of aggression in response to temporal variation in availability suggests that the stimulation of the presence of food observed by Kalleberg (1958), Keenleyside and Yamamoto (1962) and Mason (1966) is overruled by some internal mechanism that assesses food availability over a relatively long time period. If fish responded to sounds of feeding in adjacent tanks this may blur differences between adjacent regimes within the same trial, but differences between separate trials should still be apparent.

In the 1-h(x24) regime it is not known if steelhead were feeding at night or with the same efficiency as during the day. The buildup of uneaten food observed below the mesh on the bottom of the tank would indicate that less feeding occurred at night. So also do the low growth, high variability, and high mortality observed in these fish (Chapt. III). The observed high levels of aggression are therefore consistent with the hypothesis that aggressive maintenance of feeding territories should increase with decreasing levels of food availability (Slaney and Northcote 1974, Dill 1978b, Hixon 1980).

The short-term changes in the amount of aggression observed indicate that juvenile steelhead also assess food availability over shorter time periods. The observation of these changes in the random feeding regime indicates that this is a response to the feeding itself and not simply due to learning of feeding times (see Chapt. VII). Since changes occurred almost immediately after food presentation, and in some cases before it, and since the fish normally fed for several minutes, this fine-scale mechanism is probably not an internal mechanism that detects the amount of food eaten but rather a sensory assessment of the presence of food in the environment. Figure 29 suggests that the height of aggressive peaks may be proportional to meal size, as observed by Mason (1966) in coho salmon. The apparent breakdown of the pattern at 0.5-h intervals may indicate a minimum length to aggressive periods.

Why juvenile steelhead should respond in opposite fashions to long term and short term food availability is unknown. The major discussion of short term increases in aggression following feeding has centered on attempting to explain post-feeding peaks as an artifact of experimental method, rather than investigating any possible adaptive significance (Keenleyside and Yamamoto 1962, Symons 1968). While a perception of increased food availability may cause a territory holder to maintain a smaller territory, the same environmental change should influence a non-territory holder to attempt to hold a territory. Within a closed experimental system feeding should therefore result in at least a temporary instability since more fish are active, and hence more likely to come into proximity, and more fish are provided with incentive to gain a territory. Subordinate juvenile steelhead have been shown to have very little chance of overthrowing dominant individuals (Abbott et al. 1985). There should be very little incentive to challenge a dominant when there is no additional food available. A condition when there is more food available than a dominant can use or defend may offer better chances of success. The ability of these fish to learn a regular feeding schedule with considerable accuracy may reinforce this behaviour; the learning of the timing of presentation of food is logically indistinguishable from the learning of the time of no food, and there would be little incentive to increase social standing if it is known that there are no immediate rewards to be obtained.

From the point of view of the dominant it may be relatively wasteful of energy to defend a feeding territory when it is known that there will be no food in it for a considerable period of time. Alternatively, it may be efficient to defend a territory on a full stomach when the resources are available and the perceived size of the defender is larger (Abbott et al. 1985). If there is more food present than can be eaten by a dominant, a dominant can still increase its relative fitness by preventing competitors from feeding after it is satiated (Wilson 1975). In both cases, the long periods of almost total inactivity observed during the long inter-feed intervals of the infrequent feeding regimes would suggest that some food is necessary to make aggression a worthwhile expenditure of energy by either dominants or subordinates.

Any discussion of strategies of aggression is hampered by lack of knowledge of how aggression in initiated. In the salmonid literature aggressive acts are implicitly scored and reported as a characteristic of an interaction initiated by the dominant. Ethologists have long realised that social behaviours are often arranged in complicated reaction sequences (Tinbergen 1951) in which appropriate responses are required for the full complement of behaviours to be exhibited. In this respect it is presently unknown to what extent the delivery of an aggressive act is a result of the dominant's internal motivational state or to what extent it is a response to an action committed by the subordinate.

Rowell (1974) considered whether the dominant or subordinate was the cause of aggression in primate hierarchies. Reasoning that you "can't chase someone who won't flee", she calls upon observations of "provocative cringing" apparently eliciting attacks from otherwise uninvolved dominants. Little is known of the ethological function of salmonid subordinate behaviours such as "hunching" (Abbott et al. 1985) and displaying dark coloration. It has not been effectively shown that they fulfill the classic ethological function of deflecting or reducing dominant aggression and it is possible that they may identify subordinates as susceptible to attack; hunching subordinates were attacked more frequently than fish in a normal posture. Rowell also contends that dominant behaviour is more similar to the normal behaviour of individuals and that it is the subordinate which alters its behaviour. A difficulty in this approach identified by Wade (1978) is that the characteristics of a relationship do not lie in either of the individuals alone (i.e. can you flee if no one's chasing you?). However, Wade does acknowledge that the subordinate may have some degree of control over the interaction.

Another explanation of increased aggression following feeding is provided by the theoretical and experimental work of Ebersole (1980). Although an energy maximizer's territory size is generally considered to decrease under conditions of increased food availability (Dill 1978b, Hixon 1980), a static, decreasing or increasing territory size may result depending on the shape of the cost curve relative to the benefit curve (Schoener 1983). An increase is likely to be the case when the benefits of a larger territory increase faster than costs, such as travel. Depending on the decision rules used by subordinates in attempting to acquire territory, the artificial predator-free confines of experimental facilities may meet this criterion.

VI. PATTERNS OF AGGRESSIVE ATTACK IN JUVENILE STEELHEAD

INTRODUCTION

As aggressive animals functioning within a dominance system, juvenile steelhead require a mechanism by which contests are decided and the dominance system mediated. Animals may settle disputes by direct, possibly damaging fighting (escalated fighting) or by more economical, ritualised forms of aggression (conventional fighting) (Maynard Smith and Parker 1976). Displays are used as means of competing for a resource or dominance position in a non-damaging manner, but these can, however, escalate into direct physical combat (Parker 1974). Juvenile steelhead, in common with most other juvenile salmonids, employ visual displays of form, colour, and movement. In escalated conflicts these displays are replaced by fighting in the form of nips (Chapman 1962).

Since Hoar's (1951) comparative work on juvenile Oncorhynchus spp., the behaviour of several species of salmonids in both aquaria (Newman 1956, Keenleyside and Yamamoto 1962, Yamagishi et al. 1981) and streams (Kalleberg 1956, Chapman 1962, Jenkins 1969) has been observed and described. Behaviour of Salmo gairdneri was first described by Stringer and Hoar (1955), and Hartman (1965) described the behaviour of stream dwelling juvenile steelhead. However, with the exception of work on reactive distance (Cole 1976, Dill 1978a, McNicol and Noakes 1984), the form of these behaviours has not been quantified. Nipping is potentially the most damaging behaviour and parameters of this behaviour may be indicative of the costs of aggression which, if sufficiently high, may reduce growth. Salmonids of hatchery origin commonly have damaged fins (Slaney and Harrower 1981) which may affect post stocking survival, increase the likelihood of disease, or make fish less acceptable to consumers.

The purpose of this study was to measure the direction, site and result of nipping on juvenile steelhead trout and to compare patterns of aggression to observed patterns of fin damage. A serendipitous observation of "mouth-fighting", a previously unrecorded behaviour in trout, is also reported and described.

METHODS

Observations were made of groups of 8 aquarium-held juvenile steelhead. These fish comprised growth trials 1 and 2 of the growth experiment described in Chapter III. Videotaping of these groups is described in Chapter V. Data from the two groups were pooled for analysis.

One hundred random points on videotape were selected and the tape monitored until an aggressive bout occurred. A bout was characterized by the occurrence of a nip. If both fish delivered nips the bout was classified as reciprocal, and if only one of the pair delivered nips, non-reciprocal. Bouts were considered to have ended when the fish ceased to orient to each other.

Previous to administering a nip a fish would pause, orient towards the recipient and then charge, generally in a straight line. Slow motion and stop action were used to isolate the point of initiation of a charge. A straight line was then passed through the eye and tail of the aggressor. The point where this line contacted the recipient was recorded according to the diagram in Fig. 30 (inset) and assumed to be the point at which the aggressor aimed it's nip. Slow motion and stop action were used to isolate the point of contact in each bout. The body section on which a fish received a nip was recorded as with aim site. Charges that missed actual contact were included if part of a series of completed attacks. Eighty non-reciprocal bouts comprising 175 aims and 157 nips, and 20 reciprocal bouts yielding 76 nips and 79 aims were viewed.

The resulting distributions of aims or nips were compared to a model distribution. For the model I assumed that any point on the fish had a random, or equal, chance of being scored. Thus, the relative area of each body section in Fig. 30 (inset) equalled the expected relative number of scores (aims or hits) for that body area.

The two dimensional nature of videotape analysis may have introduced error into the results. While measurement of attack contact area should be relatively unaffected, variation of position in the third dimension would affect the accuracy of measurement of aim site. However, there should not be any consistent directional bias. Aims that occurred when the attacker was at an extreme angle towards or away from the plane of the screen were disregarded.

Fin damage of fish in growth trials 1,2,4, and 5 (Chapter III) was recorded at the conclusion of the growth experiments by examining them under a dissecting microscope. Growth trial 3 was omitted as these fish showed obvious fin damage when they were obtained from the hatchery. If fins were split or more than 1/3 of a fin was estimated to be missing, damage was classed as minor. When more than 1/3 of a fin was estimated to be missing damage was classed as severe. Scale loss and damage to the head (including jaws and gills) were scored for occurrence but not for severity.

RESULTS

In reciprocal bouts both aims and nips were most frequently directed at the dorsal fin and anterior area of the body. The distribution of both aims and nips were different from the random model (X^2,P<0.001) but were not significantly different from each other at the 0.05 level (Fig. 30). Non-reciprocal aims were most frequently directed at the posterior areas of the body and at the dorsal fin (Fig. 31). The distribution was significantly different

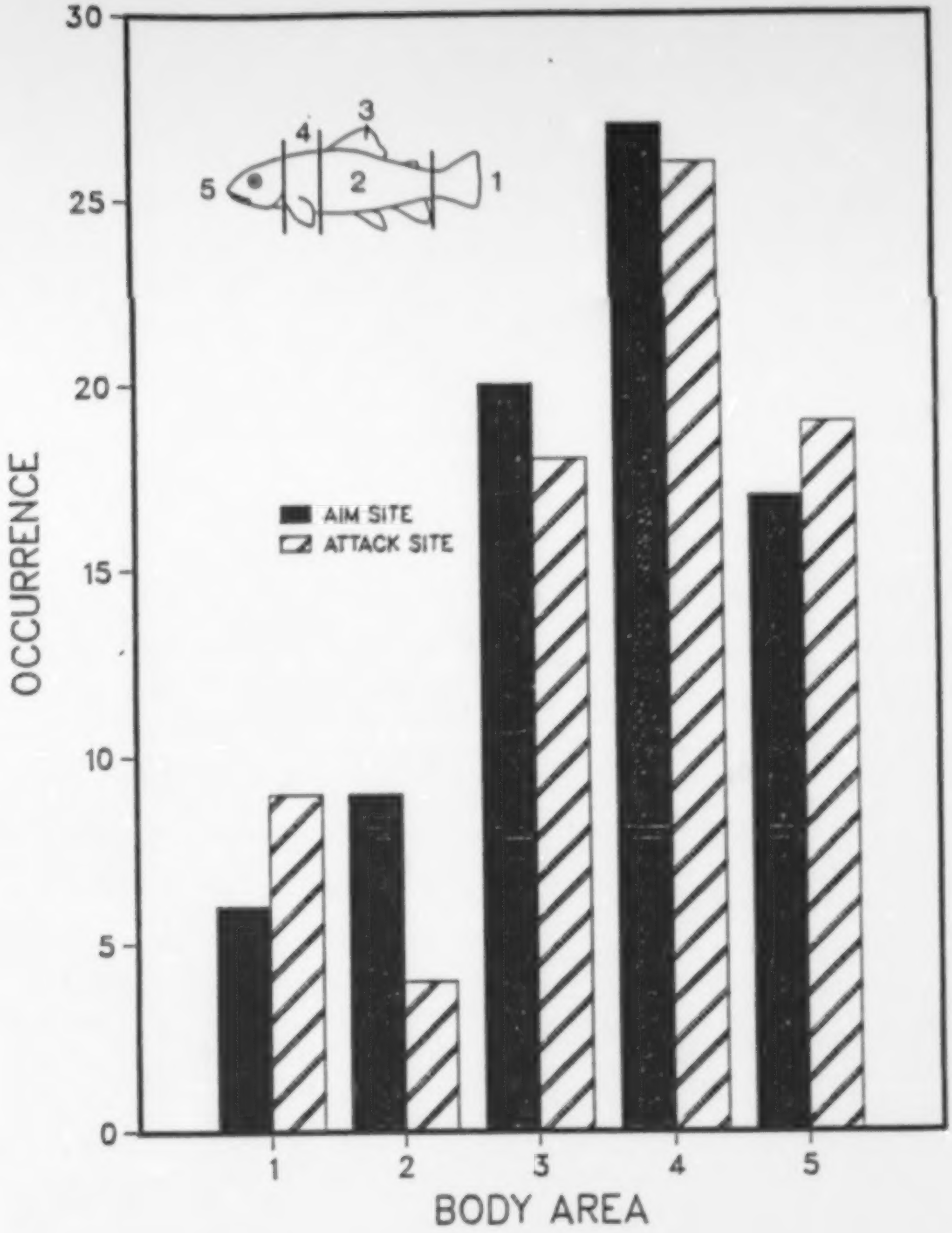

Figure 30. The distribution of aims and attacks (nips) in reciprocal aggressive bouts in juvenile steelhead.

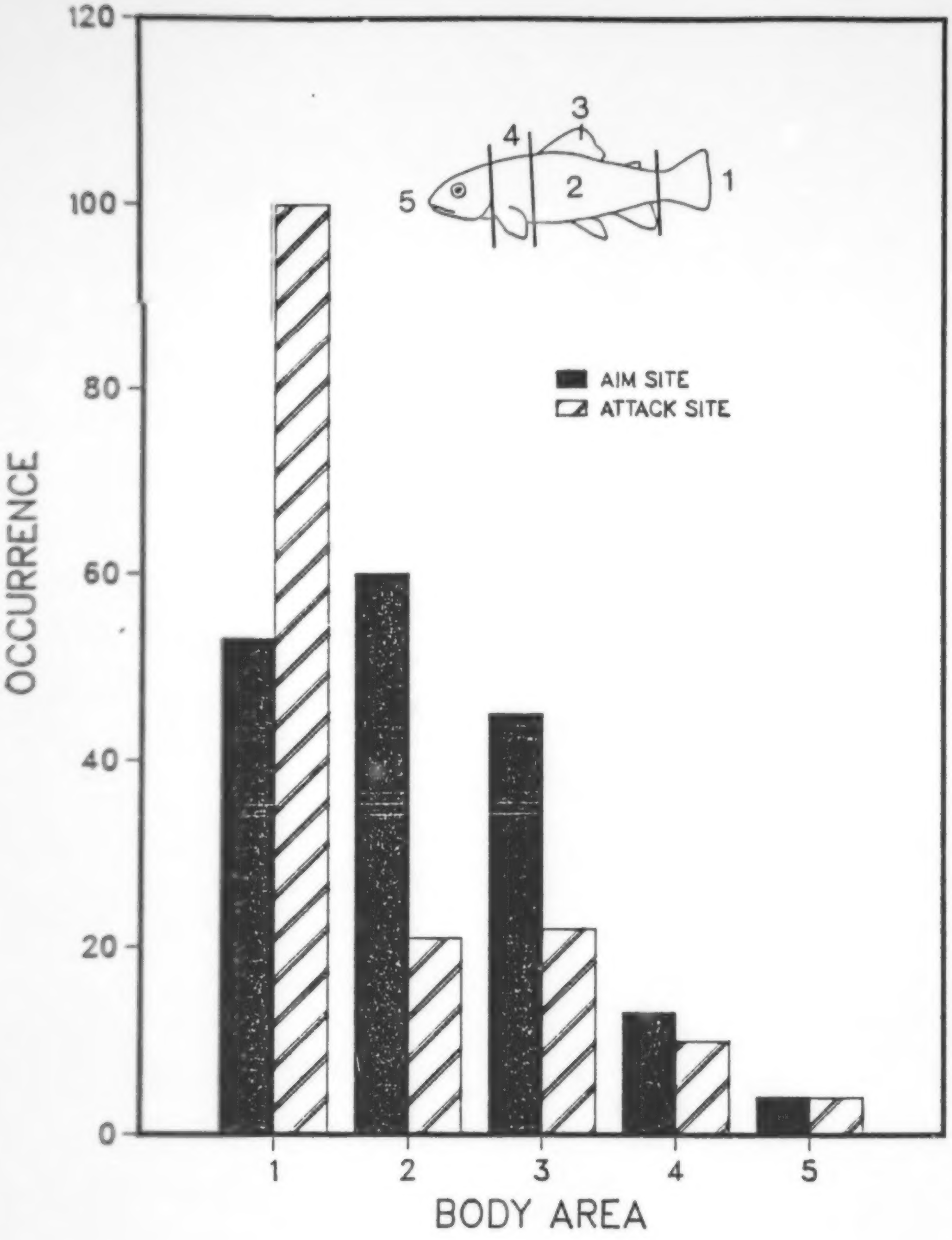

Figure 31. The distribution of aims and attacks (nips) in non-reciprocal aggressive bouts in juvenile steelhead.

from random (X^2,P<0.001) and also different from the distribution of aims in reciprocal bouts (X^2,P<0.001). Nips in non-reciprocal bouts were primarily recorded at the caudal fin and with decreasing frequency on the anterior regions. This was significantly different from a random distribution, the pattern on non-reciprocal aims, and of reciprocal nips (X^2,P<0.001 in each case).

In both grouped growth experiments the dorsal fin suffered the highest occurrence of minor damage. The pectoral and caudal fin were the second and third most damaged (Fig. 32). The occurrence of severe damage followed a similar pattern. No cases of damage to the anal fin were recorded. In both cases the distribution was significantly different from random (X^2,P<0.001).

Mouth fighting: In the course of videotaping growth trials 1 and 2 as described in Chapter V, fish were observed to exhibit a previously undescribed behaviour. On three occasions, two of which were on camera, fish ended a prolonged, reciprocal conflict by grasping each other's jaws and then "wrestling" by pulling, pushing and twisting. This was termed "mouth fighting" (Fig. 33). These interactions occurred between vigorous similar-size fish that appeared to have been contesting dominance of the tank. Mouth fighting occurred after intense bouts of fighting involving 37 and 77 nips/combatant (videotaped bouts). These nips were directed mainly at the head and pectoral fins as the fish circled. In two instances pairs ceased nipping while facing one another and then closed and locked jaws. This was done at a lower speed than when charging. In a third case the mouth locking occurred quickly in the course of a series of mouth-to-mouth nips. Fish remained locked for 27, 53, and 63 s. After releasing, one fish would swim away snapping its jaws and shaking its head and assume a quiescent position near the surface of the tank with other subordinates. In the course of analysis of subsequent videotapes three more instances of mouth fighting were observed; all followed a similar pattern.

DISCUSSION

In reciprocal aggressive bouts juvenile steelhead aim and nip sites corresponded closely and were concentrated on the dorsal fin and anterior body regions. Non-reciprocal bouts showed a pattern of aims directed at the dorsal and caudal fins but nips were concentrated more towards the posterior of the body.

The differences observed may simply be due to the retreat of one fish in the non-reciprocal bouts. Swimming away from the attack would cause the nip to contact behind the aim site. Alternatively, juvenile steelhead may employ different fighting tactics depending on the response of the opponent. The different reciprocal and non-reciprocal aim sites suggest such a change in

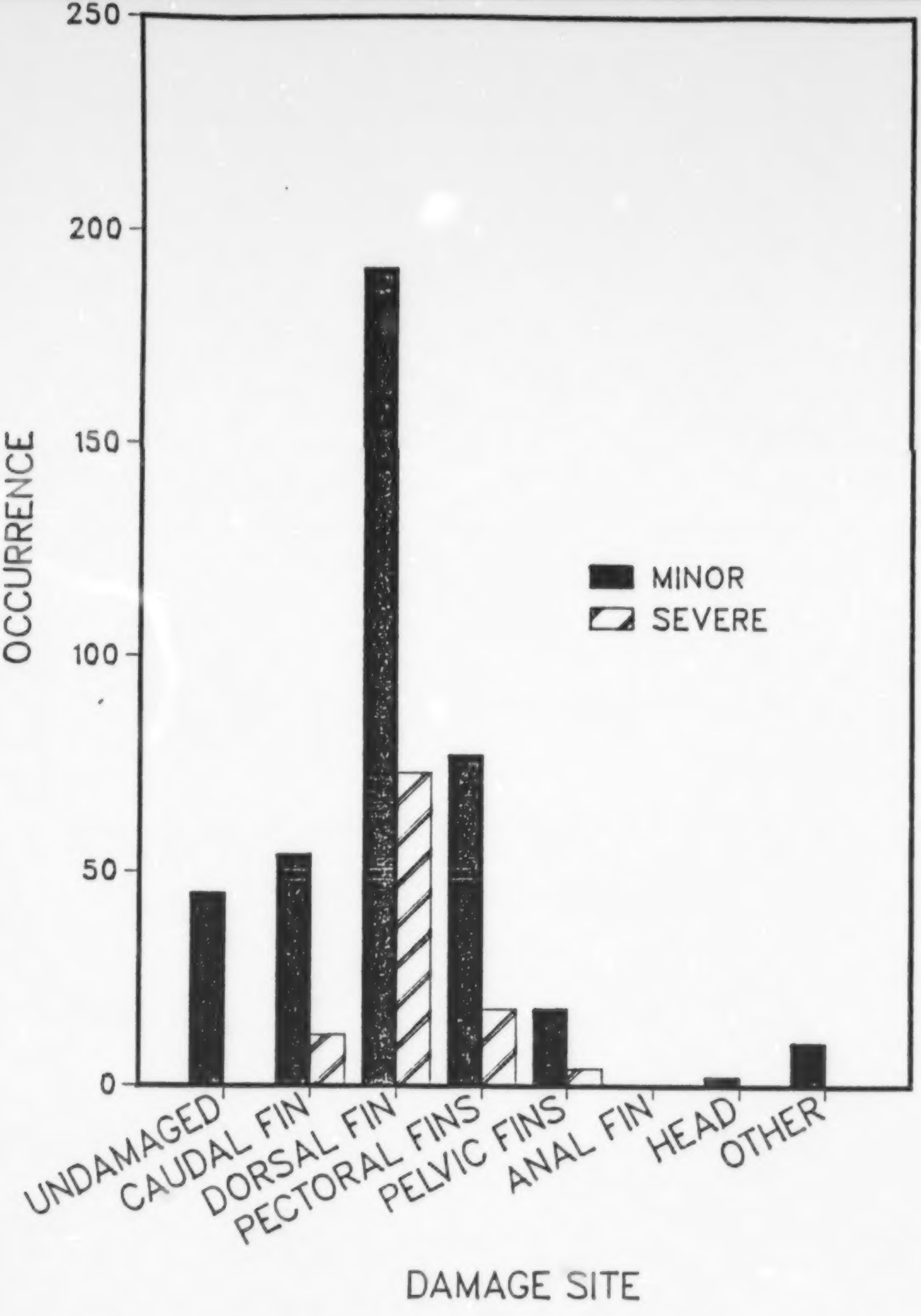

Figure 32. The occurrence of physical damage in juvenile steelhead trout. Minor damage is an estimated loss of <1/3 fin. Major damage is an estimated loss of >1/3 fin.

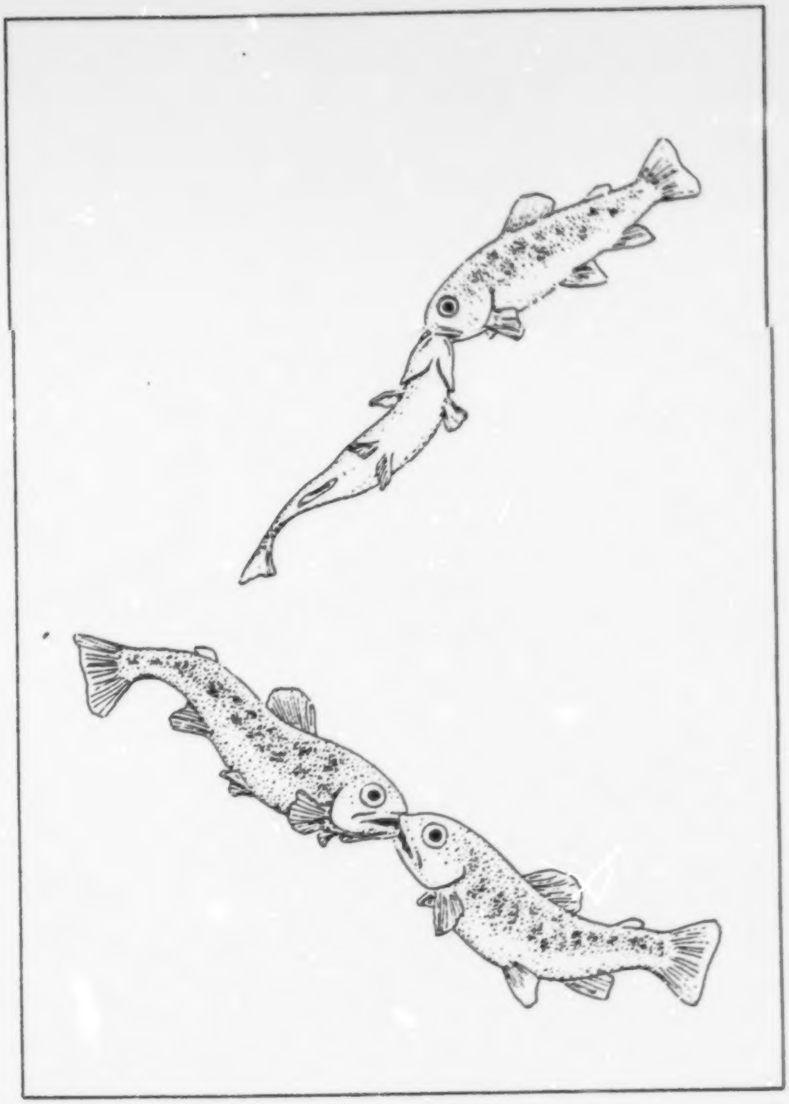

Figure 33. Mouth fighting in juvenile steelhead. Outlines traced from video tape.

tactics as aim site should be relatively unaffected by target movement. Recipients rarely moved until the attack was initiated. It cannot be determined absolutely whether head or tail nips are more damaging but because nips to the head may cause damage to the gills, eyes, and mouth parts, they may be more dangerous and thus represent escalation. Fish were often observed to shake their heads after receiving nips there.

Literature reports of juvenile salmonid fighting behaviour generally describe nips as being directed at the caudal area, e.g., by juvenile coho salmon (Chapman 1962), and by Atlantic salmon (Keenleyside and Yamamoto 1962). Stringer and Hoar (1955) stated that nips usually occurred close to the base of the tail in Kamloops (rainbow) trout but acknowledged that this may be due to the rapid retreat of the recipient. Gibson (1981) observed biting at the flanks and caudal peduncle in four species of juvenile salmonids. Newman (1956) reported that fighting rainbow trout and brook charr would attempt to grasp the pectoral or dorsal fin of the opponent. It was noted that these fish were held at high density and that return nips were common, a situation corresponding to the reciprocal bouts of this study.

Orientation and damage to the dorsal fin may be expected if the dorsal fin is more conspicuous, more accessible, easier to grasp or more delicate than other fins. The juvenile steelhead dorsal fin may be spotted, have a reddish hue and a white border at the tip, making it conspicuous. As such it may function in conflict as an aggressive releaser. Many juvenile salmonids show an erect dorsal fin in aggressive displays and a depressed fin in submissive postures (Newman 1956, Keenleyside and Yamamoto 1962, Chapman 1962, Jenkins 1969).

The complete absence of damage to the anal fin may indicate that it has little signal function or is for some reason less susceptible to attack. Dominant fish tended to hold in the centre of the tank at mid-depth or higher. Thus, many attacks were oriented downwards. Underwater observation of pen-held juvenile steelhead showed the most common attack to be a charge of two to three body lengths to nip the dorsal fin of a deeper fish (Chapter II). If this is the common attack behaviour it would make contact with the anal fin unlikely.

Several reciprocal bouts featured a previously undescribed behaviour or juvenile trout. Mouth locking, although a common aggressive and courtship behaviour in centrarchids and cichlids (Greenberg 1947, Baerends and Baerends-van Roon 1950), is not common in salmonids. MacPhee (1961) reported that both juvenile coho salmon and largemouth bass (Micropterus salmoides) locked jaws while dominance was first being established, presumably when intensity of aggression was high. R. Konopacky (Idaho Cooperative Fishery Unit, University of Idaho, Moscow, ID, pers. comm.) observed mouth-to-mouth contact of juvenile chinook salmon

Oncorhynchus tshawytscha as territories were being established in a circular stream channel. Well conditioned, dominant steelhead in the present study were observed to have red lower jaws which may have a display function. It is not known if this behaviour is relatively damaging to the combatants, but it appeared to be effective in ending the bout.

Fin damage in laboratory aquaria was concentrated on the dorsal fins as would be expected from the observed attack behaviour. This damage was similar to that observed in floating pen rearing facilities (Chapters II and VIII). Fin damage has been reported as a problem frequently affecting the culture of fish intended for commercial sale or for stocking in a sport fishery (Novotny 1980, Moring 1982). Dorsal fin size has even been used to distinguish wild from hatchery steelhead (Washington State Dept. of Game, 1984 sport fishing regulations). Fin damaged fish have a low angler acceptance (Whitlock 1974), probably display lower growth if stressed or if energy is being expended on repair of damaged tissue, and have greater susceptibility to bacterial fin disease (Schneider and Nicholson 1980). Damaged dorsal fins on lake pen-held fish were visible as white lines on their backs. Fish in pens with little fin damage were relatively hard to detect. This may lead to differential predation following stocking. In addition the loss of fins may result in decreased manoeuvrability.

Fish culture literature has generally attributed reduced fins to erosion or "rubbing" (Schneider and Nicholson 1980, Gibson 1981, Moring 1982). While Boydstun and Hopelain (1977) observed startled steelhead rubbing their sides on net pens, it is hard to see how dorsal fins would commonly contact abrasive surfaces. Given the correspondence between attack sites and observed fin damage in aquaria and floating pens in this study, aggressive interaction may be the major cause of fin damage in hatchery salmonids.

VII. HIERARCHY STABILITY AND ANTICIPATORY AGGRESSION

INTRODUCTION

The postulate that social behaviour results in different growth rates within a group due to an inequitable distribution of resources requires that observed aggressive behaviour be consistently non-randomly distributed amongst individuals. This will result in dominants accruing benefits and subordinates suffering losses. For aggression to cause growth depensation in the week-long growth tests of Chapter II, it is necessary to assume that a fish with a high aggressive output in a 30 s observation period would be likely to show high aggression, relative to other fish, in any other observation period, i.e., that position in the hierarchy is constant over time. Constancy of social order in juvenile salmonids has been shown in both experimental and natural situations (Newman 1956, Yamagishi 1962, Jenkins 1969, Bachman 1984). However, due to my inability to recognize individual fish, it was not possible to establish in Chapter V that the same fish functioned as dominants in each observation period, or that dominance hierarchy coincided with size rank.

Implicit in the hypothesis that feeding causes aggression is the assumption that aggression follows feeding. Work by Adron et al. (1973) and Landless (1976) shows that salmonids are capable of learning feeding times. If this is the case in the present study, then some of the observed aggression may have been due to the anticipation of feeding.

One purpose of this experiment was to investigate the stability of dominance hierarchies of eight juvenile steelhead (as used in Chapts. III and V) within a sampling day and also on a day-to-day basis. More specifically, the purpose was to determine the likelihood of a dominant in one sample continuing as a dominant in other samples, during the same day or week, and also to determine whether they grew faster than the subordinates. A second purpose was to establish whether food-linked aggression was due solely to the presentation of food or if fish were behaving aggressively in anticipation of a learned feeding time.

METHODS

Excess fish (approx. 100) of group 8 (Chapt. III, Table 1) were maintained in a 136.2-l flow through aquarium for 30 days. Fish were fed Silvercup commercial food twice daily, with occasional live food, under 96-lx illumination on a natural photoperiod. The fish used were thus approximately 55 days old and socially experienced at the start of the experiment. After a 2-day starvation period to eliminate food from the gut, 50 fish were anaesthetized with MS 222 and their wet weights and lengths measured. Eight fish of similar weight (0.6564 - 0.9368 g) were selected from isolated recovery vessels, and examined for identifying features. Those that were not distinctively marked (3) were re-anaesthetized and cold branded as described by Everest and Edmondson (1967). To minimise damage, a number "1" was applied at varying angles at the same location on one side of the fish. After isolated recovery overnight, branded fish did not appear to act differently from unbranded fish (branded fish were subsequently ranked first and second in the hierarchy). The eight experimental fish were installed in a 45-l flow-through aquarium at 10 C under a 11.5-h photoperiod (96 lx). Fish were fed twice daily at 1100 and 1500 h. Total ration of Silvercup was 10% of wet fish weight. Fish were screened from movement in the room and fed remotely.

On the first day after fish were placed in the experimental tank they were observed for 20 minutes and aggressive acts recorded for each fish individually on a Datamyte 800 event recorder as in Chapter V. In addition, it was possible to record lateral and frontal displays. Recorded characteristic marks and brands were found satisfactory for individual identification. On day 5 individual rates of aggression were recorded during 28, 5-min observation periods throughout the day. On day 6 the fish were not fed but individual aggressiveness was again recorded during 28, 5-min periods. Observation periods were at irregular intervals throughout the day but clustered about the two feeding periods. Fish were then starved 2 additional days, anaesthetized and reweighed. Although no food was presented on day 6 the term "feeding time" will still be used.

RESULTS

Summed ranks of each fish on days 5 and 6 are plotted against rank on day 1 in Figure 34. Rank on day 1 is based on the total number of aggressive acts given by each fish in the 20-min observation period. On days 5 and 6, rank within each 5 min interval was based on the number of aggressive acts performed, and overall hierarchy position for day 5 and day 6 was assigned according to the sum of ranks attained during each day's 28 observation periods. A comparison of ranks between sample periods on each of these days showed that individual fish were strongly associated with characteristic hierarchy positions (Friedman 2-way analysis of variance, P<0.001) on both days.

Although the overall distribution of rank was different from day 5 to 6 (X^2,P<0.01), positions 1 (alpha) and 2 (beta) were held by the same fish. A similar situation exists with regard to the changes from the preliminary rank assessment on day 1: alpha and beta positions were held by the same fish 4 and 5 days later, but otherwise only position 7 (on day 5) and 4 (day 6) were again held by the same fish. The alpha and beta fish grew faster than the other fish (Table 8).

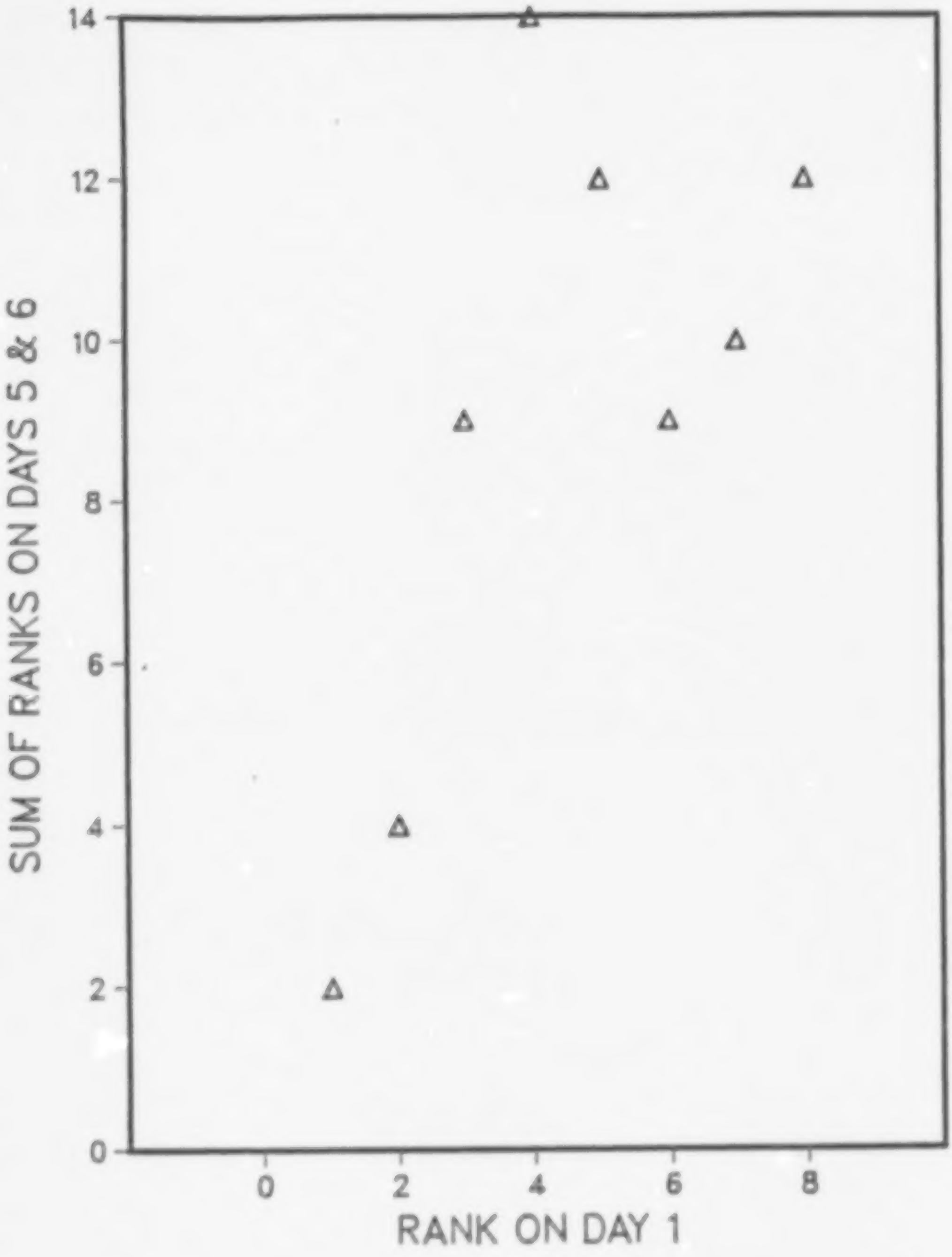

Figure 34. The relationship between the sum of ranks on days 5 & 6 and the rank on day 1 in a group of eight juvenile steelhead.

Table 8. Initial weight and growth rates of experimental fish.

Rank on Day 6	Initial Weight (g)	Final Weight	% Increase/ Day	G_s
1	.8348	.9845	3.5	.0105
2	.9368	1.0505	2.43	.0075
3	.6564	.7102	1.64	.0046
4	.7229	.7569	.94	.0027
5	.9234	1.0188	2.07	.0064
6	.6807	.6800	-.02	-.00006
7	.7026	.6998	-.08	-.0002
8	.9134	.8790	-.75	-.0024

Aggression on day 5 showed two peaks immediately followingfeeding (Fig. 35A). Aggression appeared to increase slightly before both feedings but decreased when food was present. At this time fish were occupied searching for and consuming pellets. Aggression dropped to minimal levels within 2 h following both peaks.

On day 6, major aggressive peaks occurred approximately 0.5 h before "feeding" and major drops in aggression coincided with the normal feeding times. At this time the fish were nosing about on the bottom, yawning, snapping, and holding near where food would arrive. Aggression increased immediately following "feeding" time and then remained high throughout the day (total recorded aggression for day 5 was 2174 acts and for day 6, 4827 acts). The first "prefeed" aggressive peak resulted largely from fighting between fish in hierarchy positions 5 and 3, and between fish in positions 1 and 3. At one point the latter two engaged in 4.61 min of continuous reciprocal nipping, and the data point at time 3.75-h (Fig. 35B) underestimates the true number of acts. The second "prefeed" peak represented the persecution of one fish by several higher ranking fish.

DISCUSSION

The alpha and beta positions in a hierarchy of 8 fish were found to be stable between sampling periods within one day and from day-to-day over a period of 6 days. All positions in the hierarchy were associated with particular fish on each of the two days on which periodic sampling was conducted. Several investigators have reported the stability of observed hierarchies in salmonids and these results support the conclusion that hierarchy positions, especially alpha and beta, are persistent.

Newman's (1956) observations of a mixed species population of wild salmonids showed hierarchy positions to be unchanged over a period of 15 days. The outcome of interactions between juvenile coho was found to be predictable in groups of up to five fish (Chapman 1962). Yamagishi (1962) recorded dominance position in 2 groups of 6 rainbow trout for 6 weeks during which only 4 and 9 position reversals occurred. Jenkins (1969) observed manipulated and natural populations of trout (S. gairdneri and S. trutta) in streams and found rank, size, and spatial position to be strongly associated and predictable for individuals. In 3 groups observed over one month, 95%, 97% and 98% of outcomes of encounters were predictable based on the assigned ranks of each fish. Bachman (1984), although rejecting conventional explanations of social interactions based on territory or hierarchy formation, found success in aggressive interactions and position fidelity to be consistent for individuals.

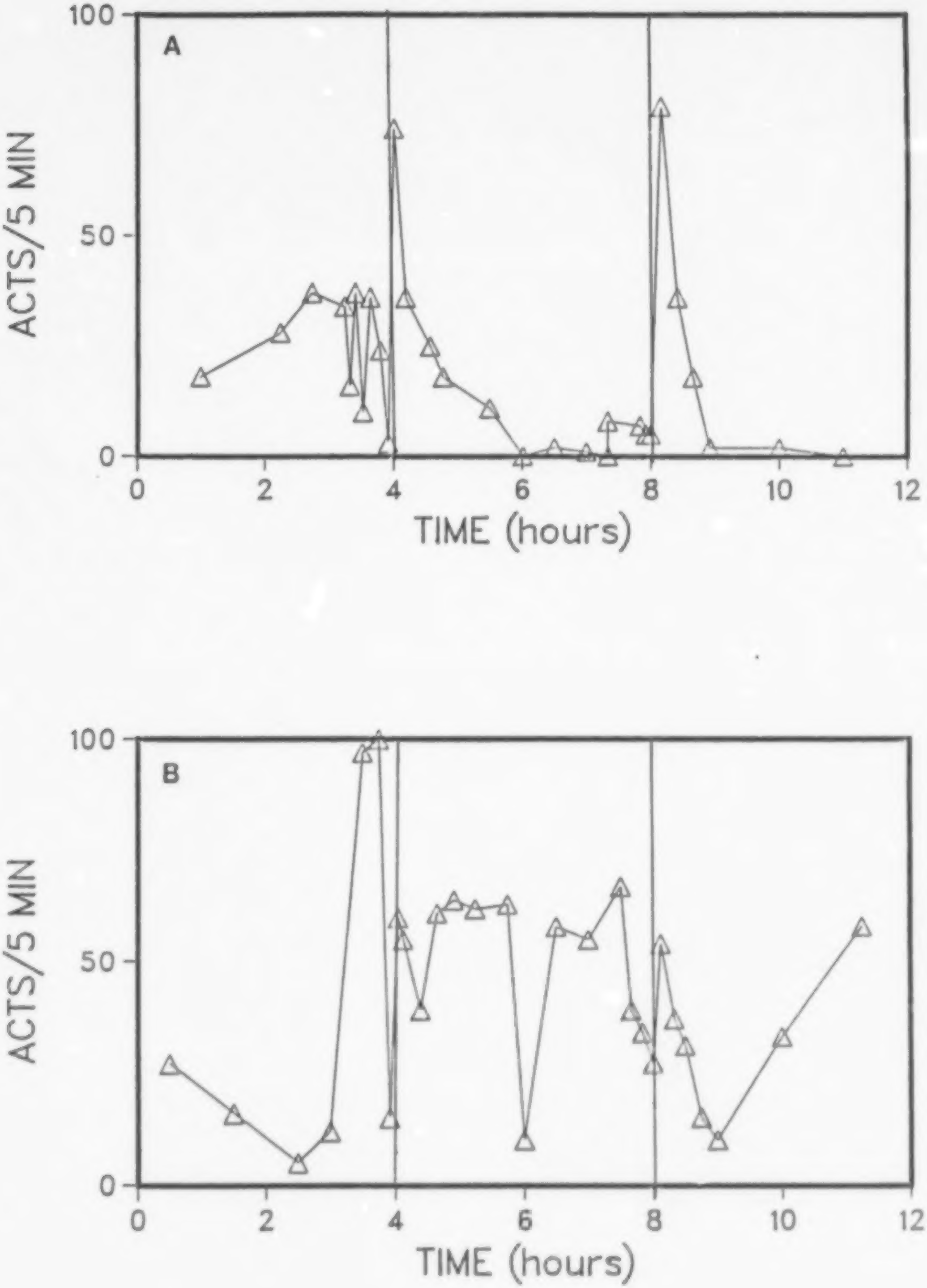

Figure 35. The time courses of aggression on days 5(A) and 6(B). Vertical lines indicate feeding times.

Although hierarchy stability cannot really be estimated over the short time scale analyzed here, the results generally agree with previous studies in showing that the relationship between individuals is not random, and that alpha and beta positions are extremely stable. Relatively low stability in the lower ranks of this group may have been affected by the choice of fish of similar weights. This would be expected to reduce stability.

That growth advantages accrued to high ranking fish is clearly illustrated in Table 8. This has also been a common observation, with Yamagishi (1962), Carline and Hall (1973) and Li and Brocksen (1977) establishing close relationships between dominance, food intake and weight gain in juvenile salmonids. Because even slightly larger fish have a higher probability of winning initial encounters (Abbott et al. 1985), weight ranking in Chapter III probably reflected behavioural rank.

Aggression rose prior to the regular feeding time on both days 5 and 6 indicating that the fish were able to monitor time and learn that some event (presumably the introduction of food) was associated with a particular time. Pre-feed levels of aggression on day 6 were extremely high. The first of these peaks cannot be considered an experimental result as no manipulation had taken place to this point. The continuous nature of the aggression during the first peak makes this point appear to be an anomaly.

During "feeding" time on both days there was a drop in aggressive activity. On day 5 this was due to the fish being pre-occupied with feeding. On day 6 the fish were observed engaged in search behaviours normally associated with feeding. The fishes' timing was exact within the accuracy used in daily feeding.

Aggression rose following the normal "feeding" time whether or not food was presented. This had a time course similar to that of the 12-h feeding regimes shown in Chapter V and generally similar to other time courses when inter-feed intervals were greater than 1h. The major difference between post-feeding aggression on days 5 and 6 was that the day 6 peaks were not as high and did not extinguish; as a result total daily aggression was more than twice as high. Although previous investigators have differed on whether feeding causes overall aggression to increase (Newman 1956, Yamagishi 1962, Keenleyside and Yamamoto 1962) or decrease (Symons 1968, 1971, Slaney and Northcote 1974), all authors working on the time course of aggression have reported a post-feeding peak. Only Mason (1966) working on coho salmon reported an anticipatory rise and an actual drop during feeding. Mason also reported that the level of post-feeding aggression was proportional to the amount fed. Present observations of higher aggressive peaks when fish were not fed do not support Mason and are consistent with Slaney and Northcote's (1974) findings.

This experiment established that fish observed as dominants in successive samples in Chapter V were likely to be the same fish, and that it was likely that the dominant fish had been enjoying the material advantages of dominance over the period of the growth experiment. In fact, all positions in the hierarchy were stable from sample-to-sample if not day-to-day, and alpha and beta positions were stable over 6 days.

VIII. TESTS OF FEEDING REGIMES IN HATCHERY FACILITIES

INTRODUCTION

The effect of fish behaviour on the production of juvenile salmonids in hatcheries has received little attention. The problems of size of facilities, numbers and density of fish are compounded by the speed of movement and difficulty of identifying and tracking individuals. The science of ethology, excepting the study of colonial insects, is generally practised upon individuals, small groups, or easily separable subgroups (Altmann 1974). Fish culturists have rarely been able to observe their animals and so have been required to observe the large scale, final effects of their activities, e.g., conversion of food and mean weight. As a result they are unable to separate any social effects. Most major aquaculture texts (e.g., Bardach et al. 1972) fail to supply any mention of social behaviour beyond certain instances of cannibalism and growth depensation in Penaiid shrimps.

Intensive culture of salmonids has been shown to have strong and marked effects upon fish behaviour that may be important when fish are removed to a wild situation. Differences in vertical orientation, predator avoidance, reaction to cover and substrate choice, food choice and recognition, and aggressive patterns of wild and hatchery fish have all been recorded and may have far reaching effects on survival and growth (Schuck 1948, Miller 1958, Vincent 1960, Moyle 1969, Fenderson and Carpenter 1971, Sosiak et al. 1979). However, social behaviour may also influence the crop of fish at the hatchery facility, whether measured as hatchery production or as survival to the fishery or spawning. Possible effects in large scale facilities include slower growth rates, increased growth variability, and stress affecting growth or susceptibility to disease.

Growth variation may be of particular importance in fish culture. Disparity in size may be an advantage where fish are harvested directly from the hatchery depending on market demands. In systems where fish are released to the wild, a threshold size is often required. For a "put and take" fishery (no assumed or desired survival (Everhart et al. 1975) only those fish above the legal size limit are useful products, therefore, the less the variance, the lower the average size required to maximize the number of catchable fish. Reduction of variance may be especially important to anadromous fish that have a threshold size for resistance to salt water and successful smolting, including coho and steelhead (Houston 1961). Depending on the processing of hatchery harvested fish, fin damaged may be disregarded, but planted hatchery fish as identified by damaged fins are held in low esteem by sport fisherman (Whitlock 1974).

Following a laboratory investigation into the effect of feeding regime on growth and aggressive behaviour (Chapts. III and V), the effects of feeding regime on growth, size variance and fish quality in pen-reared and hatchery populations of juvenile steelhead were tested. Although experiments in aquaria were designed to indicate the nature and mechanism of the effects, the results may not be transferable to full size production facilities. Several aspects of scale would suggest this; while fish numbers and dimensions may be proportional to the size of the pens, absolute size and swimming space are changed greatly, allowing longer chase and flee distances. The greater numbers probably preclude individual recognition and resulting hierarchy stability (Barnard and Burk 1979). The number of intruders is increased and the area is much larger than any economically defendable territory (Dill 1978b); in fact, food is sometimes dispersed over a larger area than a conventionally defended territory. These reasons are enough to suggest that fish in pens may respond differently from small aquarium populations and it was considered necessary to test several feeding regimes in pens.

Selection of feeding regimes was influenced by several constraints. First, the maximum growth required by production facilities dictated normal high rations. The information in the literature (reviewed in Chapt. III) suggests frequent feeding to achieve high growth which agrees with results obtained here (Chapt. III). Current British Columbia Fish and Wildlife Branch practice involves feeding at 20-min to 2-h intervals (P. Slaney, B.C. Fish and Wildlife Branch, pers. comm.). It was decided to test the extremes of this range and two alternative feeding methods in pens: (1) very frequent feeding (5-min intervals), and (2) feeding throughout the day and night (2-h interval times 24). Night feeding was selected in the event that fish are able to feed at very low light levels. In the hatchery, random intervals averaging 30 min (range 1 to 60) were compared with a control of a regular 30 min feeding interval. The effects of these regimes in production facilities were examined by measuring growth and dorsal fin damage.

METHODS

Pen Experiments:

Experiments were conducted from Oct. 1 to Dec. 1, 1982 in four, 2.44 m x 2.44 m x 2.44 m floating net pens at the Canadian Forces Base Chilliwack bridging ponds adjacent to the Chilliwack River. Four groups of 1250 Chilliwack River winter-run steelhead (1982 brood) were removed from 2275-l circular tanks at the Fraser Valley Trout Hatchery and transported by truck to the bridging ponds. Two pens designated as A-1 and A-2 were covered by a shed. Two other pens, B-1 and B-2, were covered with black polyethylene sheeting to keep the ambient light levels as similar as possible.

Fish in pen A-1 were fed at 30-min intervals, A-2 at 5-min intervals, B-1 at 2-h intervals for 24-h, and B-2 at 2-h intervals for a 12-h day. All pens received equal total daily rations delivered from suspended hoppers closed with a circular plate. Spinning of the plate at feeding time scattered feed over most of the surface of the pens. Rations of Silvercup feed were determined using Iwama and Tautz's (1981) growth equation for a 2.2:1 food to biomass conversion ratio. Water temperatures ranged for 9 to 6 C and daylength from 11.6 to 8.45 h.

Weekly sampling was conducted on 60 fish per pen. Fish were captured by lifting the net at one corner of the pen to concentrate the fish; the approximate number were then dipped out and transferred to 77-l containers. Fish were transported by truck, approximately 250 m to buildings where power was available.

Fish were anaesthetized in 2-phenoxyethanol and weighed on a Mettler P-1200 dual electric balance. Fork length and length of the first dorsal fin ray were measured and a subjective estimate of dorsal fin damage was made. Damage (estimated fin loss) was ranked on an integer scale of: 0, no damage; 1, 0 to 25% damage; 2, 25 to 50% damage; 3, 50 to 75% damage; and 4, 75 to 100% damage.

Hatchery Experiments:

Experiments were conducted from Nov. 15, 1981 to Jan. 10, 1982 in 2250-l circular flow-through tanks at the Fraser Valley Trout Hatchery. A random feeding interval was tested against a regular feeding interval at the Fraser Valley Trout Hatchery. The regular feeding regime consisted of 0.5 kg Silvercup feed per day distributed every 30 min. The random regime consisted of an equal ration distributed with an average interval of 30 min and a range of 1 - 60 min. Natural lighting prevailed and the temperature was a constant 9.6 C. Samples were taken approximately weekly by netting 60 fish which were handled and measured in the same manner as the pen-held fish.

RESULTS

Pen Experiments:

The initial average sizes of fish groups assigned to pens were significantly different from one another (ANOVA, $p<0.05$), possibly indicating an unconscious bias in technique or sampling error. The final weights were also significantly different (ANOVA, $p<0.05$) but throughout the experiment weights were similar, had a similar range and generally appeared to follow a similar growth pattern (Fig. 36). The relative ranking of groups was also inconsistent, all groups except the 5-min interval regime were ranked first on at least one occasion and all groups were ranked last on at least one occasion. In addition, all groups lost weight during at least one period. Thus, no feeding group exhibited superior growth. Growth

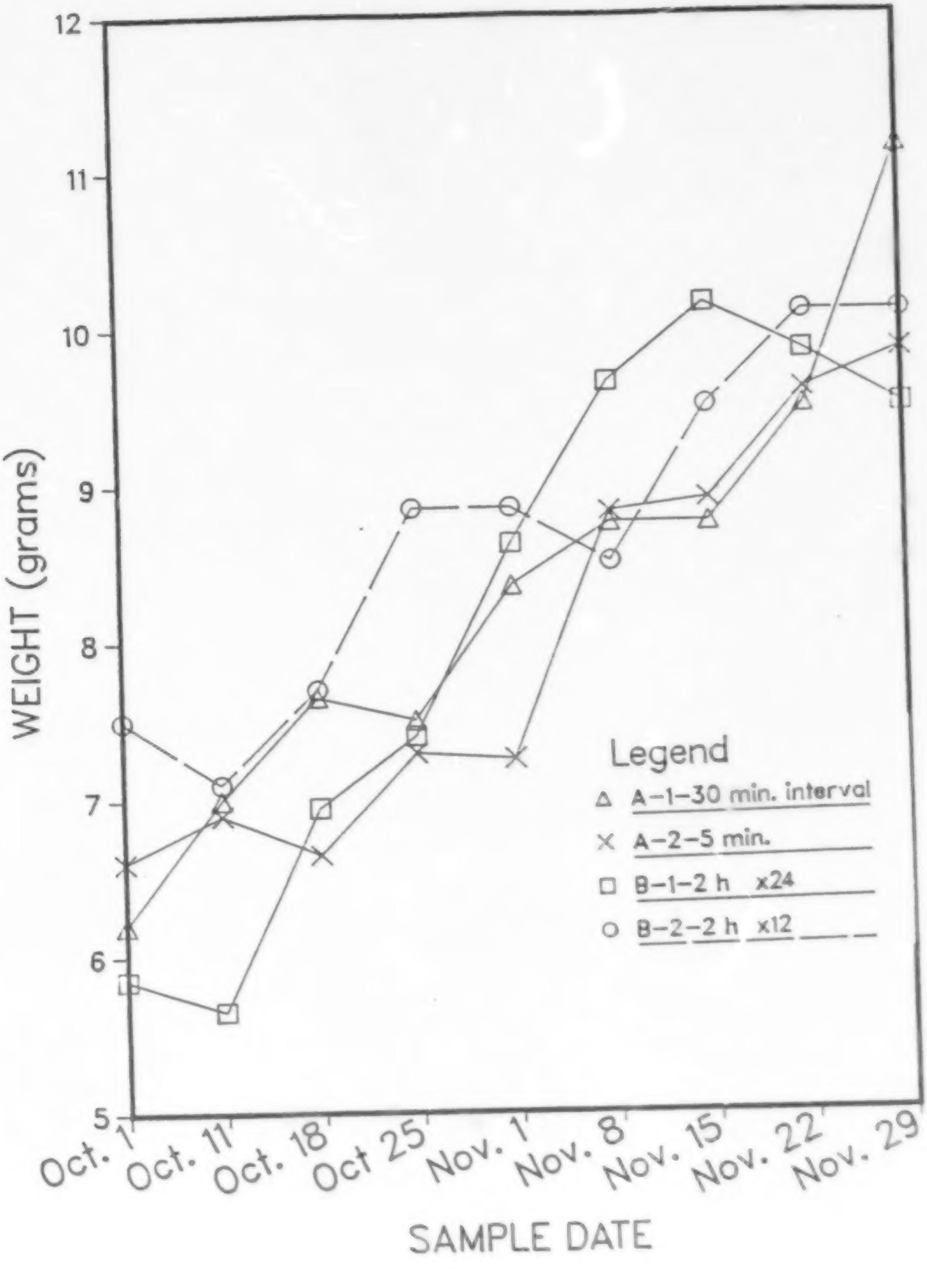

Figure 36. The average weights of groups of pen reared steelhead under various feeding regimes.

coefficients (G_c) ranged from 0.49 to 0.79.

The size variance of all groups increased with time. Variances were homogeneous at all except two sample dates (Oct. 25 and Nov. 22) (F max test, $p>0.05$), hence the use of ANOVA for testing differences of the initial and final means. Coefficients of variation were tested by F max test of squared coefficients of variation, as suggested by Lewontin (1966). No significant differences were noted except on October 25, the date of maximum range ($p<0.05$, Fig. 37). Again no consistent trend was obvious. The weight of individual fish in each of the final samples was normally distributed (Kolmogorov-Smirnov test, $p>0.05$).

Dorsal fin heights generally declined with time (Fig. 38). Fins were generally highest in pen B-2 and shortest in pen A-2. Significant differences occurred, but again no clear pattern presents itself. The subjective measure of fin damage generally agreed with the objective measure but revealed less distinction between regimes.

Hatchery Experiments:

Both groups had very similar initial weights and grew at similar rates. Weights were not significantly different at any subsequent time (Student's t test, $P>0.05$) although the random group had a significantly higher final weight ($p< 0.05$, Fig. 39). Growth coefficients were high: 1:17 (regular) and 1.25 (random). Initial weight loss of the randomly fed group coincided with a feeder malfunction. Size variances increased with weight and remained heterogeneous (F max test, $p<0.05$): the weights of randomly fed fish were less variable than those of regularly fed fish (Fig. 40). Coefficients of variation diverged steadily after the first half of the experiment and were significantly different for the last sample dates (F test of squared co-efficients of variation, $p<0.05$, Fig. 40). Both final samples were normally distributed (Kolmogorov-Smirnov test, $p>0.05$).

Fin size of randomly fed fish was always smaller than that of regularly fed fish by 0.2 to 1.2 mm (Fig. 41); the difference was significant on three occasions (Students's t test, $p<0.05$). Subjective measure of fin damage revealed less distinct differences.

DISCUSSION

Pen Experiments:

A test of four feeding regimes in floating net pens did not reveal any clear, consistent superiority or trends in measures of growth (weight), growth variation, or dorsal fin damage. Growth coefficients (G_c) were low compared to those measured at various B.C. salmonid production facilities (Iwama and Tautz 1981).

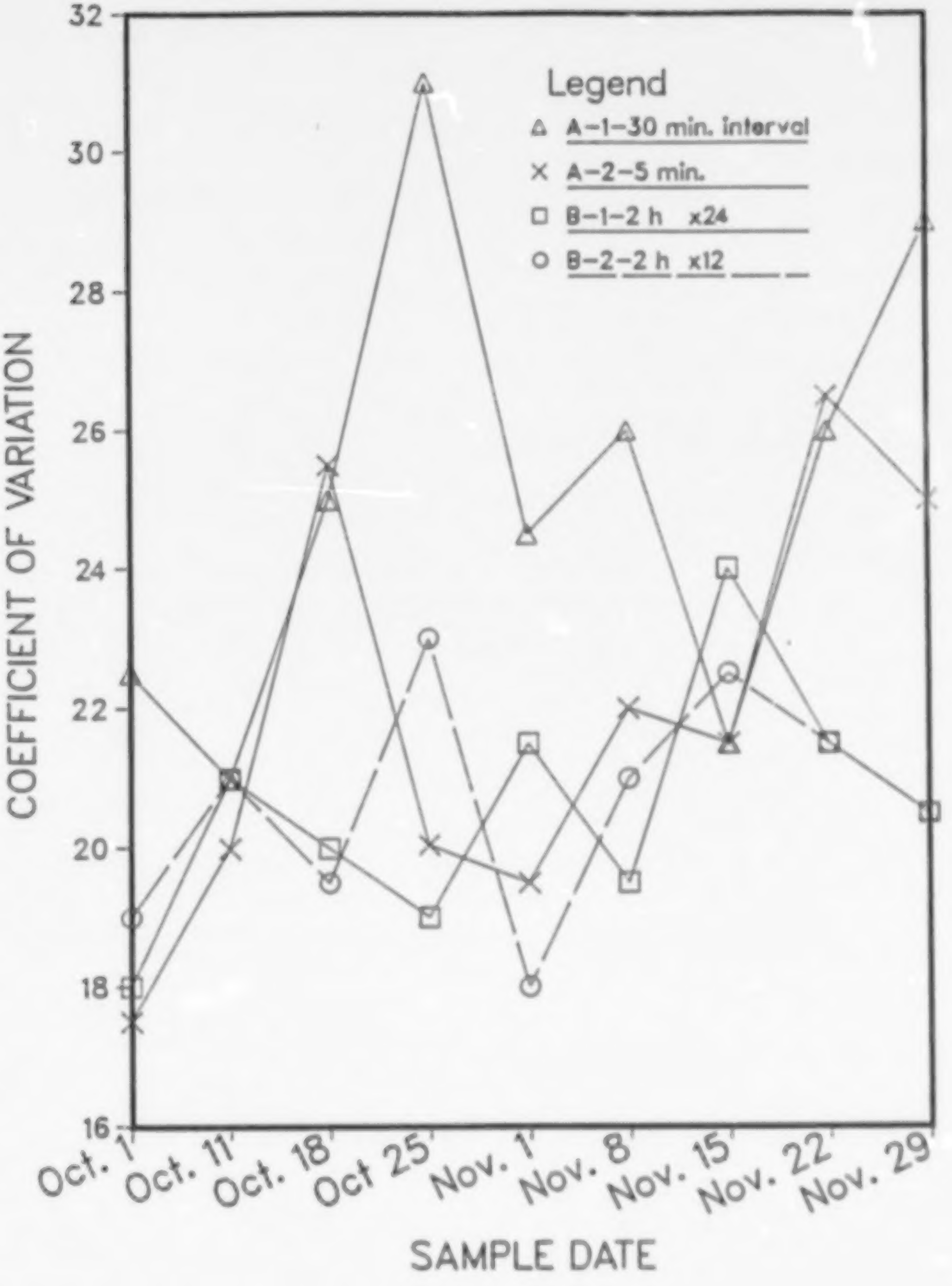

Figure 37. The co-efficient of variation of groups of pen-reared steelhead under various feeding regimes.

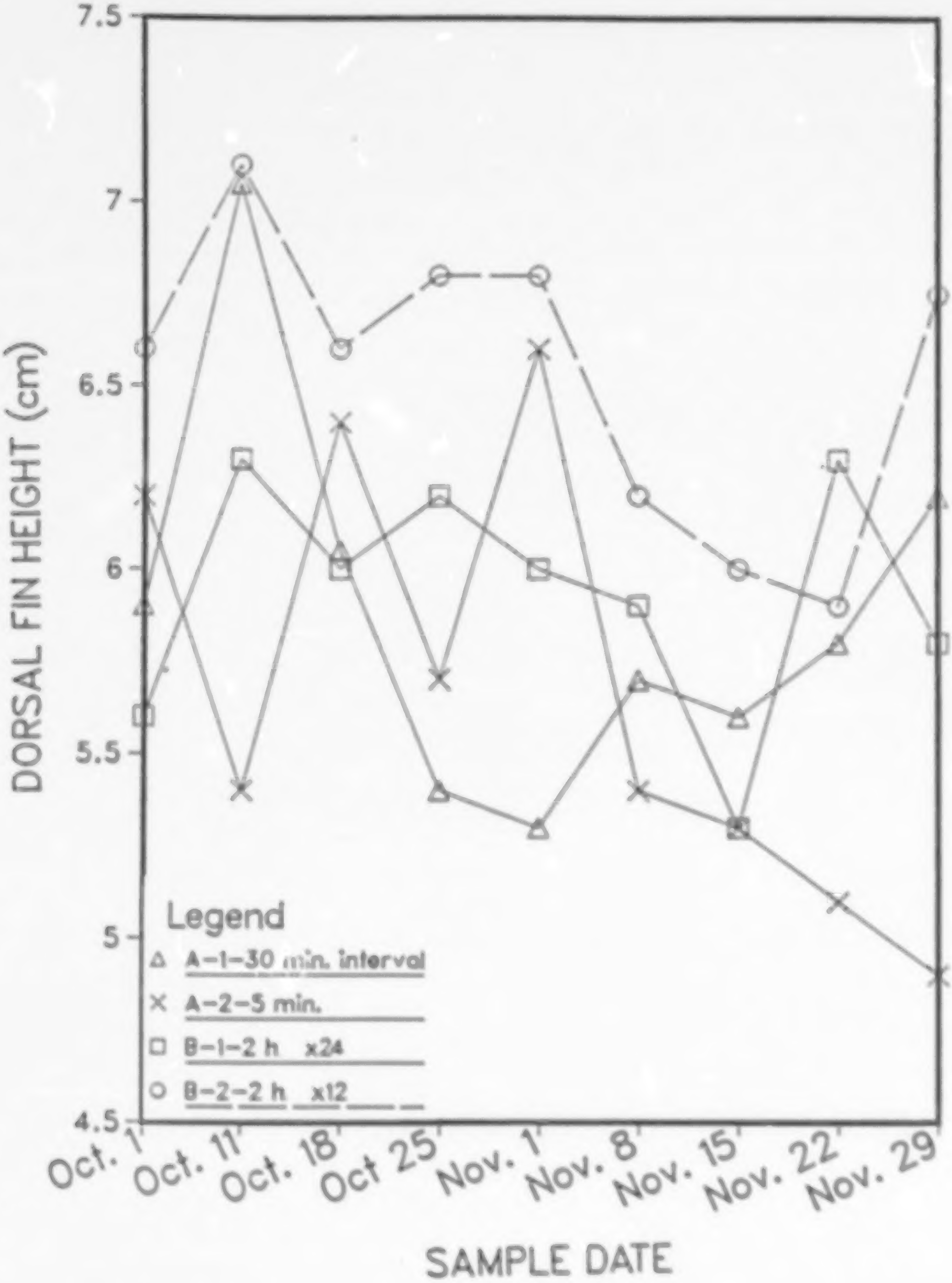

Figure 38. The average dorsal fin heights of groups of pen-reared steelhead under various feeding regimes.

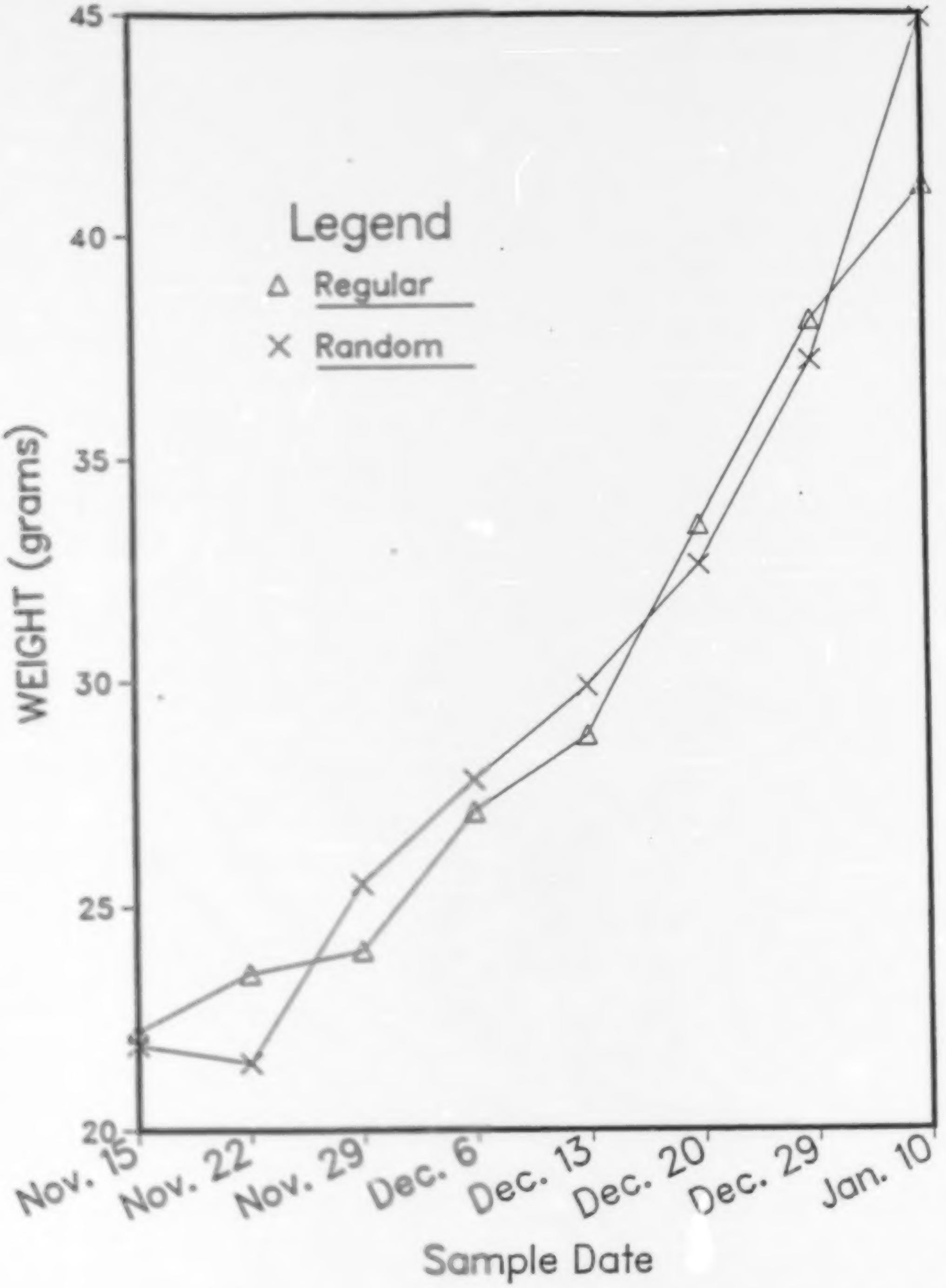

Figure 39. The average weight of 2 groups of hatchery-reared steelhead under different feeding regimes.

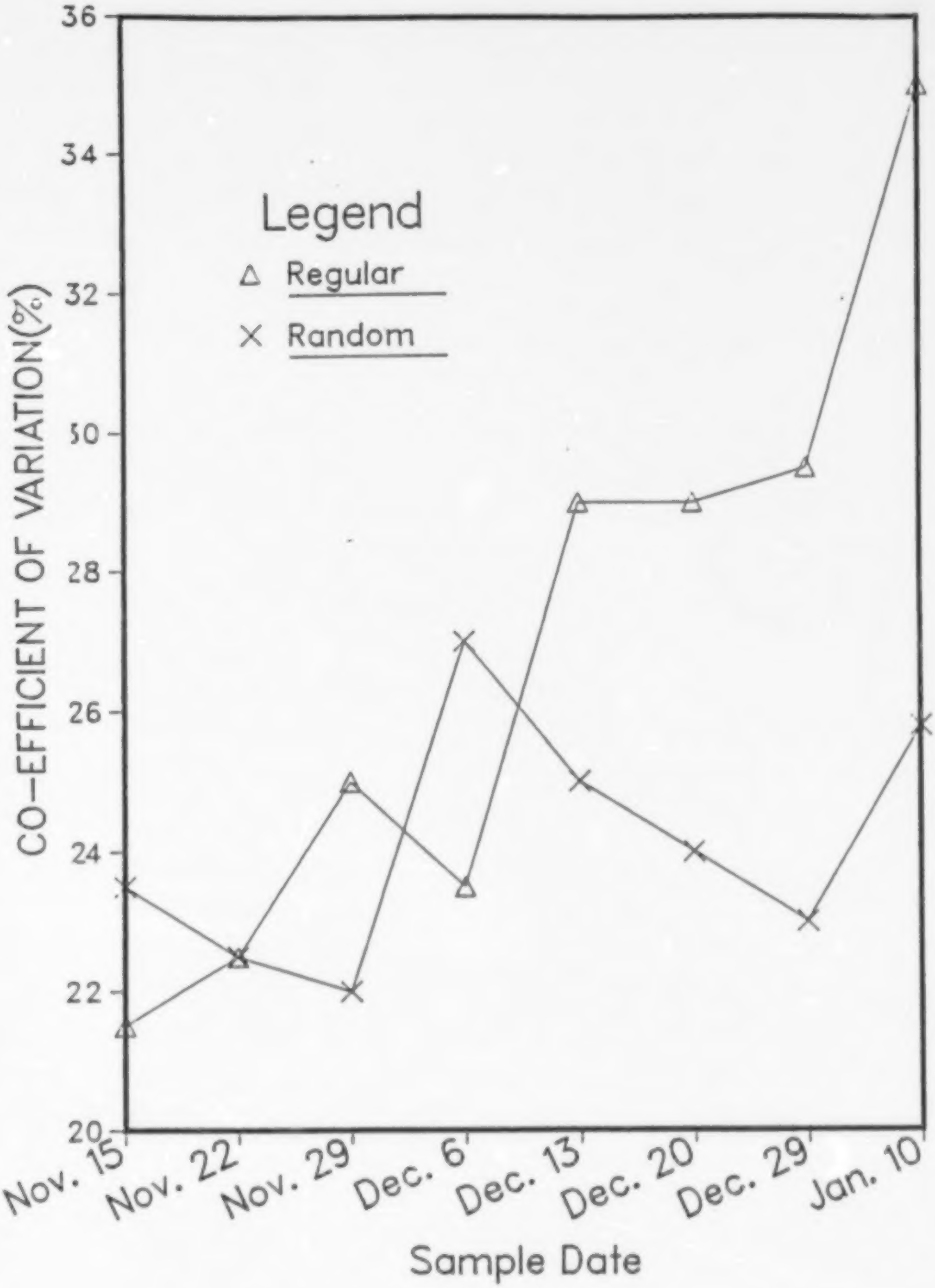

Figure 40. The co-efficient of variation of 2 groups of hatchery-reared steelhead under different feeding regimes.

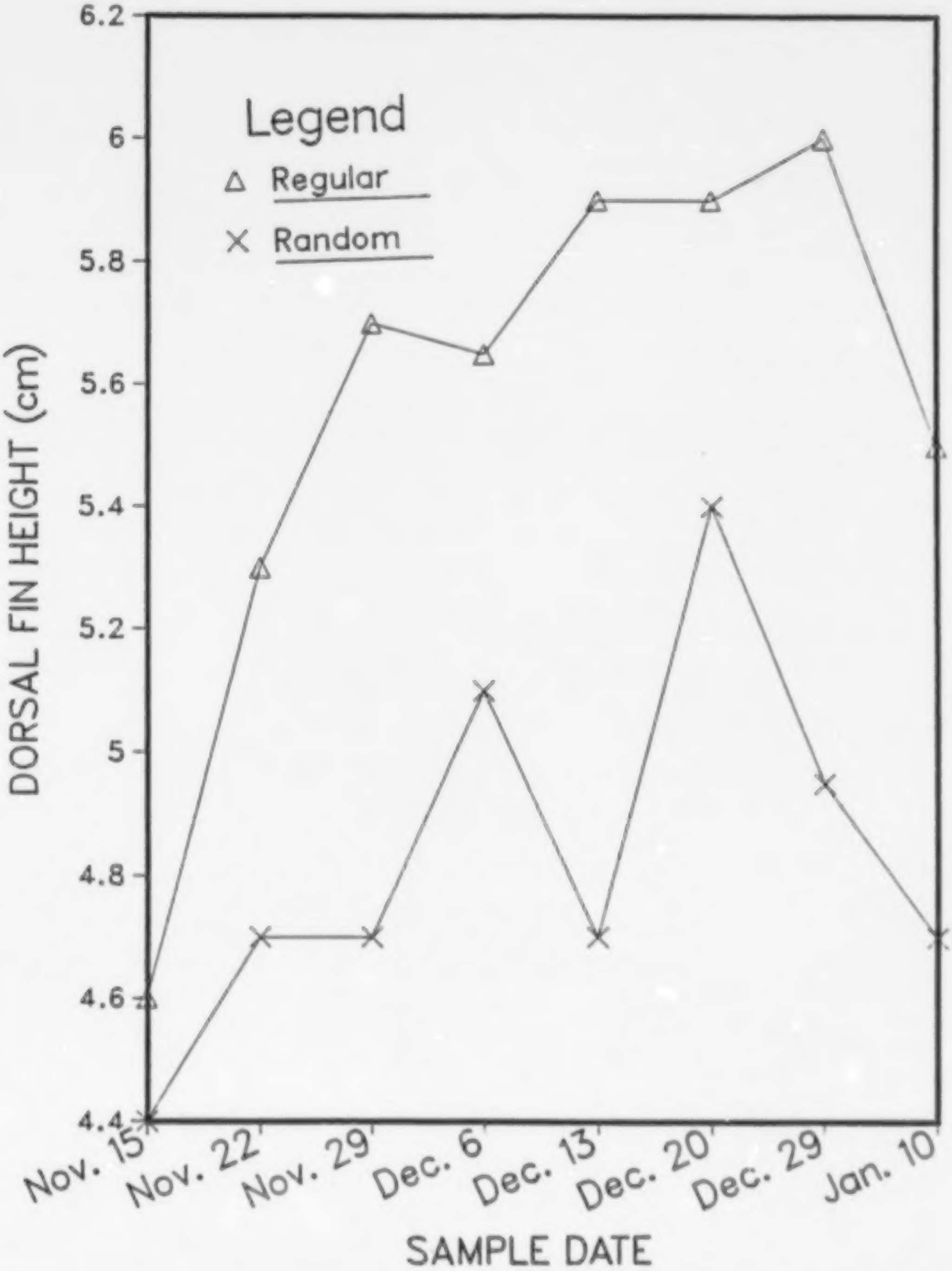

Figure 41. The average dorsal fin height of 2 groups of hatchery-reared steelhead under different feeding regimes.

However, the fish were behind hatchery weight goals at the start of the experiment and would not have reached a threshold of approximately 50 g by the smolting period. The initial differences in weight at the beginning of the experiment was due to the entire contents of a hatchery circular tank being transferred to a single pen. Although the original tanks had received similar treatment, differences obviously existed. These differences did not dictate the subsequent growth performance as relative ranking changed frequently.

The interpretation of the 2-h interval (X 24 h) feeding regime presents certain problems. Hours of daylight decreased from 11.67 to 8.45-h over the course of the experiment. After a loss of weight in the first week, consistently high growth rates were recorded until the last 2 samples. This regime could therefore be advantageous if daylight hours are greater than some threshold. Since other pens were fed for 12 h/day, 24-h feeding could be an advantage when daylight is greater than 12-h, especially if fish are fed more than can be processed in 12-h. Since the 24-h regime received approximately 1/2 of it's food during the daylight hours, this may suggest an improved digestive efficiency to maintain equivalent growth or, more probably, overfeeding in the 12-h pens.

The lack of major differences between the pens may be a result of the age of the fish. Gunnes (1976) found that grading Atlantic salmon prior to 6 months of age reduced subsequent size variability. These fish may have established certain growth characteristics prior to this experiment. The reduction in activity and growth due to seasonal effects also may account for the small differences noted.

Hatchery Experiments:

The randomly fed group performed better than the regularly fed controls. Final weight was significantly higher even though the initial weight was lower. Growth variation increased faster in regularly fed fish and was significantly higher. Fin damage, measured by dorsal fin height, was greater in the randomly fed group, thus contradicting any simple hypothesis that the amount of fin damage and growth variation should be related in the same manner to aggression.

Growth performance of both groups was excellent relative to recorded growth coefficients of steelhead in other B.C. production facilities (Iwama and Tautz 1981). Projection of this growth rate until April would give an average size of 89 g, considerably above the normal smolting threshold. Assuming that a normal distribution of size persisted, only 10% of the randomly fed smolts would be below 60 g, as opposed to 16% of the regularly fed smolts (Fig. 42). This would occur even without any further increase in coefficient of variation. If coefficient of variation also increased owing to regular feeding over the entire freshwater

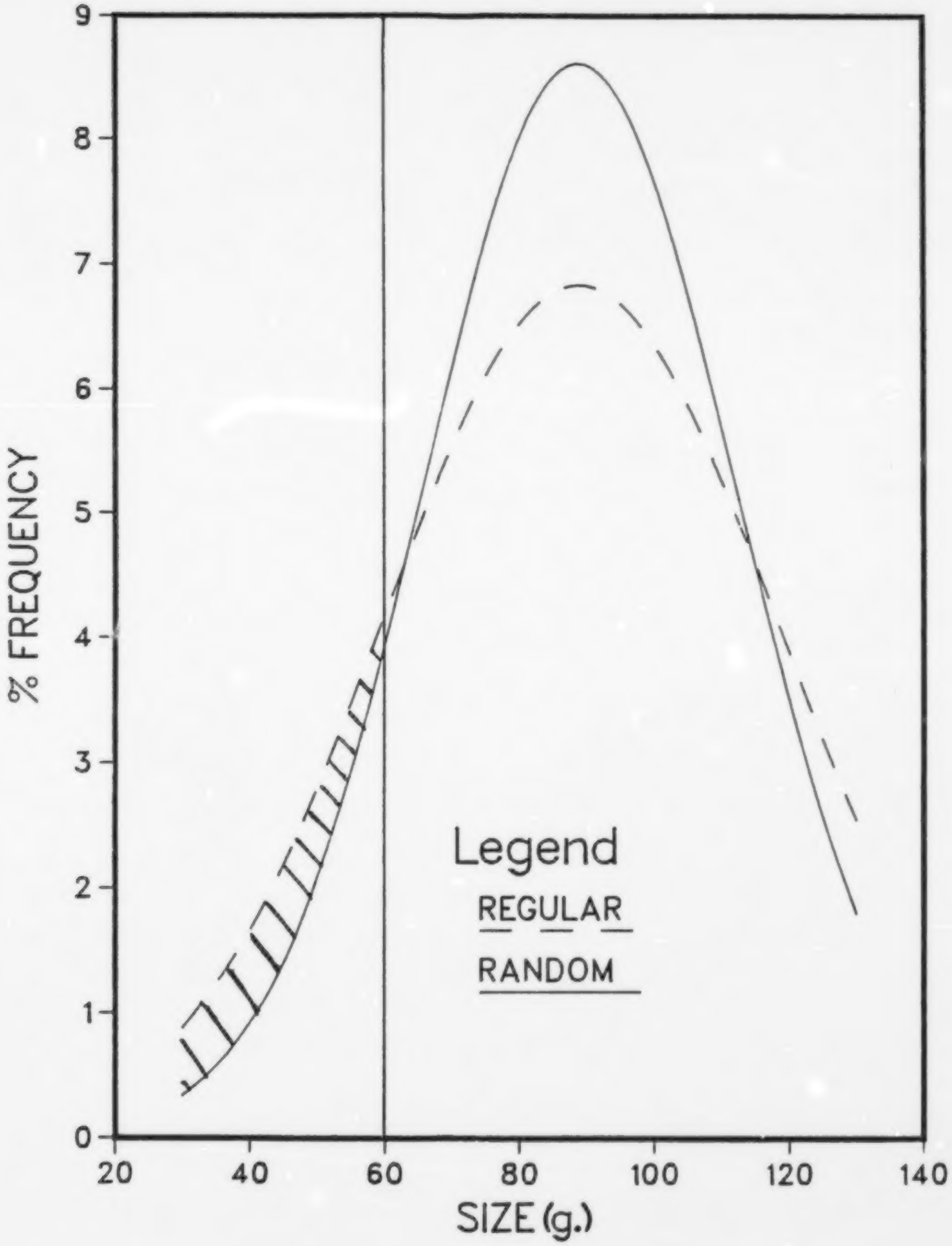

Figure 42. The projected size distributions, at smolting age, of random and regularly fed juvenile steelhead. The vertical line represents a size threshold for successful smolting. The hatched area represents the difference in smolt production.

growth period, the difference in performance would be magnified. It is to be expected that this will increase production of smolts with no loss of total size, but there are other factors to be considered in this type of analysis. These are discussed in Chapter IX.

Any recommendation of random feeding on this basis assumes that the saving achieved by uniform growth is greater than losses due to reduced dorsal fins. No work detailing the quantitative effects of reduced dorsal fins on survival is known, but the absolute difference between the two groups is only about 1 mm and the modal subjective measure of fin damage for both groups was in the 50% erosion category. The difference in this case may not be biologically significant. Only five categories were used in the subjective measure of fin damage; since this entails the observer making a guess as to how much dorsal fin should be there, a greater number of categories is not realistic. Since group averages were closely clustered in similar categories the actual measurement of dorsal fins is recommended for better discrimination of differences.

IX. CONCLUSIONS

This series of experiments has attempted to reveal some of the relationships between feeding and growth characteristics, particularly variability, and between feeding and aggression, in juvenile steelhead. Specifically this study has found that:

1. aggression occurs in floating lake rearing pens and laboratory research shows that this behaviour is responsible for observed patterns of fin damage (Chapts. II and VI.);
2. grouped fish display greater growth variation than socially isolated fish (Chapt. III);
3. social aspects other than differential food intake are responsible for some growth variability (Chapt. IV);
4. increased feeding frequency causes greater growth and less variability relative to the growth rate (Chapt. III);
5. timing of feeding does not affect total levels of aggression but does cause short term changes in aggression around feeding (Chapt. V);
6. the high ranking positions in small hierarchies are relatively stable and correlated with a high growth rate (Chapt. VII);
7. juvenile steelhead can accurately learn their feeding times (Chapt. VII); and
8. the growth and growth variability of pen-held juvenile steelhead was unaffected by the experimental feeding regimes, but under a random feeding regime growth was increased and growth depensation decreased relative to a regularly fed control group in hatchery circular tanks (Chapt. VIII).

The purposes of this concluding discussion are: to consider the usefulness of present models of optimal territory size for the purpose of generating predictions that are testable in situations as complex as the wild environment of juvenile salmonids; to investigate the function of aggression as a mechanism of resource allocation; to examine the relevance of the experimental situation to wild fish; and to demonstrate the importance of reducing growth depensation in hatchery production.

Schoener's (1983) publication was titled "Simple models of optimal feeding territory size; a reconciliation." While the models themselves are mathematically simple and brief, the predictions are not necesarily simple (Figure 6C, Table 1, Schoener 1983), and the problem of testing the array of predictions, or of choosing the right model to fit a particular test situation are anything but simple. Predictions based on food density alone are simple enough (see Ebersole 1980), but because food density and intruder pressure are inter-dependent, food density can rarely be isolated as a determinant of territory size in natural systems. Most studies of salmonid aggression have been confounded by a complex of different intruder regimes superimposed upon different experimental feeding regimes. In addition the existence of a continuum from territories to hierarchies raises the question of what is intruder pressure? Kalleberg (1958) and Puckett and Dill (1985) have described salmonid "floaters" that exist on and between territories; they are allowed to remain there as long as they exhibit non-threatening, non-aggressive behaviour. Thus it is clear that intruder pressure is not just a question of numbers but also a matter of the initiation of certain behaviours by the intruders. This returns us to the question considered by Rowell (1974) and Wade (1978) (discussed in Chapt. V.): Is it the dominant or subordinate that initiates aggression? Full understanding of territorial behaviour, in salmonids at least, must await the resolution of this question.

The reasoning behind experiments in Chapters III and IV, and much of the relevant literature, is that "aggression causes growth depensation, therefore, more aggression should cause more growth depensation". This was explicitly stated by Magnuson (1962) and Yamagishi (1962). More recent authors, while accepting that social interactions are a major cause of growth depensation, have not monitored aggression (Jobling 1982, 1983, Koebele 1985). The reduction of aggression and more economical distribution of resources is generally considered a benefit of hierarchies. Rowell (1974) challenged this viewpoint, asserting that the reduction of aggression observed as hierarchies formed in new groups was a reduction from unnaturally high levels to a normal situation. Wade (1978) argued against this assertion and Barnard and Burk (1979) provided additional theoretical evidence that a well developed social order is the most efficient means of dividing resources.

Since the experimental apparatus was so different from the natural surroundings of juvenile steelhead, it is necessary to consider whether the results hold any relevance for natural situations. Fish in this study were probably more stressed than is usual in the wild. Fish and other animals tend to have hyperactive adrenals when in captivity and in hierarchies (Rowell 1974). This and the inability to emigrate could have forced behavioural decisions not normally observed. However, I contend that the experimental environment bears similarities to certain normal juvenile steelhead habitats. Personal observation shows that immediately after hatching, steelhead approximately 25-30 mm in length are found in shallow margins of streams where there is low water velocity. The boulders or gravel there create small pockets along the shoreline that are almost isolated from the main stream. During heavy hatches of steelhead, up to six individuals may occupy a pocket at a density greater than in these experiments. For example, on May 25, 1985 a sheltered cutting in the bank of the

Stamp River was observed to contain upwards of 40 juvenile coho salmon (25-40 mm long) in a space approximately 1.3 m long, 0.4 m wide and up to 0.35 m deep. The end of this backwater, partially isolated from the main body, contained 11 fish in an area 0.4 m long, 0.2 m wide and 0.1 m deep. In 5 min, 37 aggressive acts (as defined earlier) occurred. The density in this case is considerably greater than in the experimental apparatus and the frequency of aggression comparable. Northcote (1962) reports similar aggregations of juvenile rainbow trout along the margins of streams at night. Mortality rather than growth depensation is likely to be the result of these early interactions, as Chapman (1962) and Mason and Chapman (1965) have documented the importance of success in early encounters. High density and confinement can also occur when side channels dry up and fish are concentrated in isolated pools by old cut banks or root wads. For example, I have observed a group of approximately 20 juvenile coho salmon in a pool (1.2 m in diameter and 0.3 m deep) 50 m from the mainstem of the Stamp River. These fish persisted from May at least until September, 1984. Similar situations exist for steelhead. This high density and lack of stream drift create marginal feeding conditions that are similar to the present experimental set up. I concluded from these field observations that natural conditions similar to those created in these experiments exist, at least for short but crucial periods.

Anadromous fish smolt through a physiological size window. Fish below the lower size threshold are unlikely to survive the transition to salt water and either die or remain in freshwater. Salmonids that are above the upper threshold may have an increased chance of male precocial maturity (Bilton 1978) with early return to the home stream at a smaller than normal size (Maher and Larkin 1955, Parker and Larkin 1959). Small steelhead smolts when reared in lake-pens or hatcheries are thought to remain in freshwater, rather than migrate to sea (Slaney and Harrower 1981). Any of these instances may be considered lost production from the viewpoint of fishery management. Figure 43A shows two normal curves with the same means and different variances. The advantage (difference in number of smolts above a size threshold) of a low coefficient of variation depends on the proximity of the size threshold to the mean. The difference in the number of smolts lost is given in Figure 43B. If the group average does not exceed the threshold size the group with the higher variation will actually be at an advantage. A family of curves following this pattern exists with the magnitude of the values dependent on the relative levels of variation in the two groups. A similar but inverted line could represent the effect of an upper threshold.

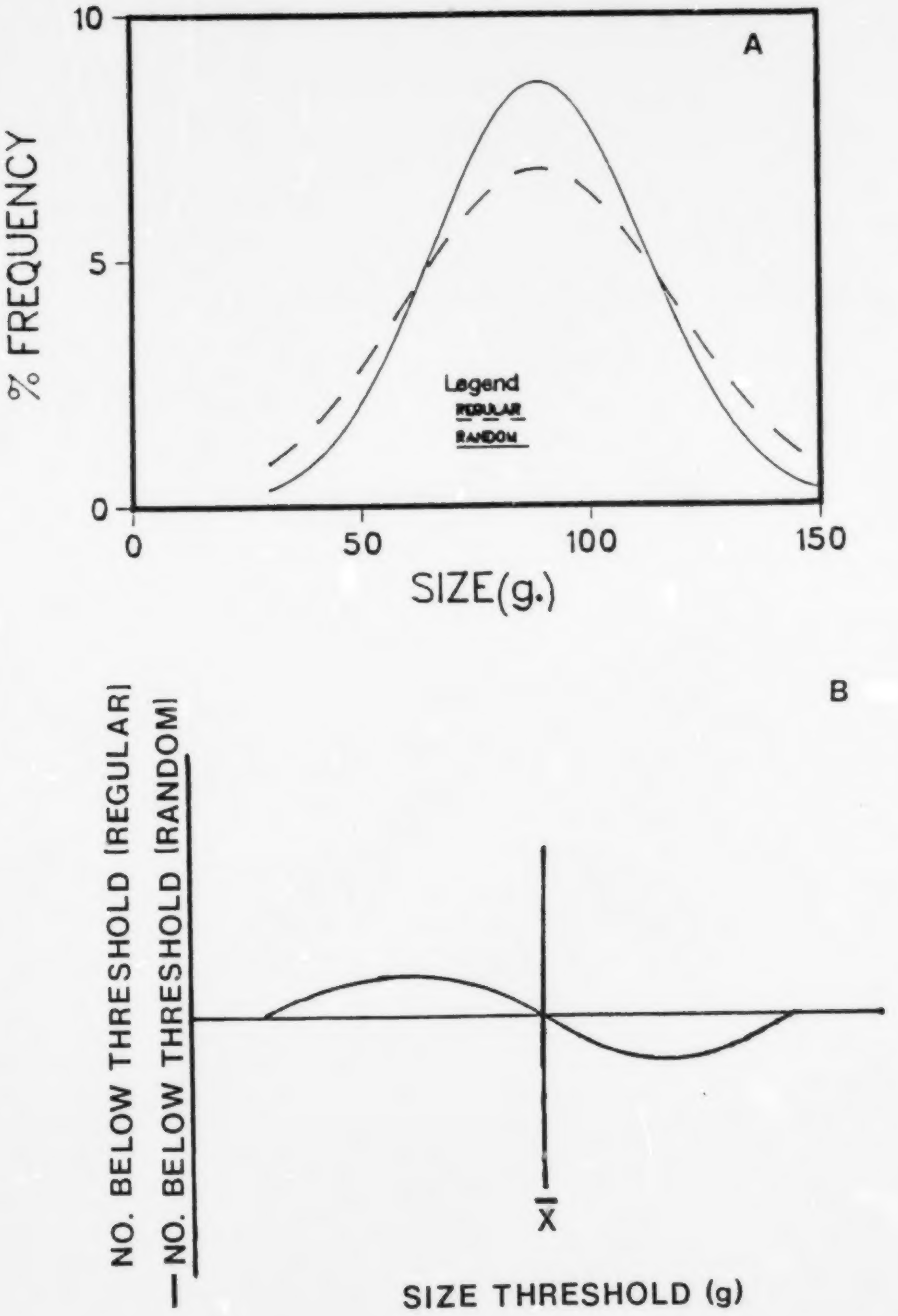

Figure 43. The effect of moving the smolt size threshold on relative numbers of fish produced by populations with different variance. A is from Fig. 42. B represents the difference in production obtained with a changing size threshold, i.e. the advantage of random feeding.

RECOMMENDATIONS

All the results from the laboratory experiments suggest that juvenile steelhead should be fed frequently for optimal growth and minimal size variability. The fact that a clear cut pattern of aggressive peaks breaks down at feeding intervals less than one hour indicates some change at the behavioural level, but the significance of this is not understood.

Because juvenile steelhead learn feeding times accurately and exhibit anticipatory aggression, random feeding may eliminate this portion of aggression. The feeding regimes of growth trial 5 are inconclusive considering the high mortality rate of this group and their generally stressed appearance. Random feedings show potential for further investigation due to the success achieved in hatchery experiments, although the logistics of feeding fish randomly may be impractical as random capabilities are not generally found on commercial fish feeders. A pseudo-random regime such as frequent, irregular hand feeding as a supplement to a regular regime may have a beneficial effect.

Production scale experiments with feeding regimes should be initiated at an early stage in the fish's life. Since fish are growing fastest (in % weight increase) at this time there should be the greatest potential for significant changes.

Although not specifically tested here, food should be distributed over a wide area to prevent concerted defence of a point source. Although it was not possible to find a correlation between growth depensation or aggressive damage and feeding regime, the potential post-release mortality due to the effects of fin damage indicate that it could be a major cause of production losses. Field studies on the effect of damaged fins on post-release survival should be undertaken to quantify the effect and determine the potential benefit of reduction of fin damage.

LITERATURE CITED

Abbott, J.C., Dunbrack, R.L. and Orr, C.D. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (Salmo gairdneri). Behaviour 92:241-253.

Adron, J., Grant, P.T. and Cowey, C.B. 1973. A system for the quantitative study of the learning capacity of rainbow trout and its application to the study of food preferences and behaviour. J. Fish Biol. 5:625-636.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49: 227-267.

Bachman, R.A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in stream. Trans. Am. Fish. Soc. 113:1-32.

Baerends, G.P., Baerends-van Roon, J.M. 1950. An introduction to the study of the ethology of Cichlid fishes. Behaviour Suppl. 1:1-234.

Bardach, J.E., Ryther, J.H. and McLarney, W.O. 1972. Aquaculture: The farming and husbandry of freshwater and marine organisms. Wiley Interscience, New York. 860 pp.

Barnard, C.J. and Burk, T. 1979. Dominance hierarchies and the evolution of "individual recognition". J. Theor. Biol. 81:65-73.

Beggs, G.L., Holeton, G.F. and Crossman, E.J. 1980. Some physiological consequences of angling stress in muskellunge, Esox masquinongy Mitchill. J. Fish Biol. 17:649-659.

Bilton, H.T. 1978. Returns of adult coho salmon in relation to mean size and time of release. Can. Fish. Mar. Serv. Tech. Rep. 832:73pp.

Boydstun, L.B. and Hopelain, J.S. 1977. Cage-rearing of steelhead rainbow trout in a freshwater impoundment. Prog. Fish Cult. 39:70-75.

Brett, J.R. 1971. Satiation time, appetite and maximum food intake of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Board Can. 28:409-415.

Brett, J.R. 1979. Environmental factors and growth. Pp 599-677 in Fish Physiology, Vol VIII. W.S. Hoar, D.J. Randall and J.R. Brett (eds). Academic Press, New York.

Brown, J.L. 1964. The evolution of diversity in avian territorial defense systems. Wilson Bull. 76:160-169.

Brown, M.E. 1946. The growth of brown trout (Salmo trutta). I. Factors influencing the growth of trout fry. J. Exp. Biol. 22:118-129.

Carline, R.F. and Hall, J.D. 1973. Evaluation of a method of estimating food consumption rates of fish. J. Fish. Res. Board Can. 30:623-629.

Chapman, D.W. 1958. Studies on the life history of the Alsea River steelhead. J. Wild. Manag. 22:123-134.

Chapman, D.W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19:1047-1080.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat. 100:345-357.

Cole, K.S. 1976. Social behaviour and social organization of young rainbow trout, Salmo gairdneri, of hatchery origin. M.Sc. thesis, Univ. Guelph. 100pp.

Dawkins, R. 1982. The extended phenotype: the gene as the unit of selection. W.H. Freeman and Co, Oxford. 307pp.

Dill, L.M. 1978a. Aggressive distance in juvenile coho salmon (Oncorhynchus kisutch). Can. J. Zool. 56:1441-1446.

Dill, L.M. 1978b. An energy based model of optimal feeding-territory size. Theor. Pop. Biol. 14:396-429.

Dill, L.M., Ydenberg, R.C. and Fraser, A.H.G. 1981. Food abundance and territory size in juvenile coho salmon (Oncorhynchus kisutch). Can. J. Zool. 59:1801-1809.

Donnelly, W.A. and Dill, L.M. 1984. Evidence for crypsis in coho salmon, Oncorhynchus kisutch (Walbaum), parr: substrate colour preference and achromatic reflectance. J. Fish Biol. 25:183-195.

Ebersole, J.P. 1980. Food density and territory size: an alternative model and a test on the reef fish (Eupomacentrus leucostictus). Am. Nat. 115:492-509.

Ejike, E. and Schreck, C.B. 1980. Stress and social hierarchy rank in coho salmon. Trans. Am. Fish. Soc. 109:423-426.

Elliott, J.M. 1975. The growth rate of brown trout fed on maximum rations. J. Anim. Ecol. 44:805-821.

Erickson, J.G. 1967. Social hierarchy, territoriality, and stress reactions in sunfish. Physiol. Zool. 40:84-90.

Everest, F.H. and Edmundson, E.H. 1967. Cold branding for field use in marking salmonids. Prog. Fish Cult. 29:175-176.

Everhart, W.H., Eipper, A.W and Youngs, W.D. 1975. Principles of fishery science. Cornell Univ. Press, Ithaca

Fagerlund, U.H.M., McBride, J.R. and Stone, E.T. 1981. Stress related effects of hatchery rearing density on coho salmon. Trans. Am. Fish Soc. 110:644-649.

Fenderson, O.C. and Carpenter, M.R. 1971. Effects of crowding on the behaviour of juvenile hatchery and wild landlocked Atlantic salmon (*Salmo salar* L.). Anim. Behav. 19:439-447.

Francis, R.C. 1983. Experiential effects on agonistic behaviour in the paradise fish, *Macropodus operculatus*. Behaviour 85:292-313.

Frey, D.F. and Miller, R.J. 1972. The establishment of dominance relationships in the blue gourami, *Trichogaster leeri* (Pallus). Behaviour 42:8-62.

Gall, G.A.E. and Gross, S.J. 1978. Genetic studies of growth in domesticated rainbow trout. Aquaculture 13:225-234.

Gauthreaux, S.A. Jr. 1978. The ecological significance of behavioural dominance. Pp 17-54 in Perspectives in Etholgy, Vol 3. P.P.G. Bateson, P.H. Klopfer (eds) Plenum Press, New York.

Gibson, R.J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*), at the juvenile fluviatile stages. Can. Tech. Rep. Fish. Aquat. Sci. 1029:116pp.

Greenberg, B. 1947. Some relations between territory, social hierarchy and leadership in the green sunfish (*Lepomis cyanellus*). Physiol. Zool. 20:267-299.

Gunnes, K. 1976. Effect of size grading young Atlantic salmon (*Salmo salar*) on subsequent growth. Aquaculture 9:381-386.

Hartman, G. F. 1965. The role of behaviour in the ecology of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 22:1035-1052.

Hixon, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115:510-530.

Hoar, W.S. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. J. Fish. Res. Board Can. 8:241-263.

Houston, A.H. 1961. Influence of size upon the adaptation of steelhead trout, Salmo gairdneri, and chum salmon, Oncorhynchus keta to salt water. J. Fish. Res. Board Can. 18:401-415.

Iwama, G.K. and Tautz, A.F. 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38:649-656.

Jenkins, T.M., Jr. 1969. Social structure, position choice and microdistribution of two trout species (Salmo trutta and S. gairdneri) resident in mountain streams. Anim. Behav. Monogr. 2:1-123.

Jobling, M. 1982. Some observations on the effects of feeding frequency on the food intake and growth of plaice Pleuronectes platessa L. J. Fish. Biol. 20:431-444.

Jobling, M. 1983. A short review and critique of methodology used in fish growth and nutrition studies. J. Fish Biol. 23:685-703.

Jobling, M. 1985. Physiological and social constraints on growth of fish with special reference to arctic charr, Salvelinus alpinus L. Aquaculture 44:83-90.

Jobling, M. and Wandsvik, A. 1983. Effect of social interactions on growth rates and conversion efficiency of Arctic charr, Salvelinus alpinus L. J. Fish Biol. 22:577-584.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout. Inst. Freshwater Res. Drottningholm Rep. 39:55-98.

Keenleyside, M.H.A. and Yamamoto, F.T. 1962. Territorial behaviour of juvenile Atlantic salmon (Salmo salar). Behaviour. 19:139-169.

Koebele, B.P. 1985. Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. Env. Biol. Fishes 12:181-188.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. Pp 23-63 in Behavioural Ecology: an evolutionary approach. J.R. Krebs and N.B. Davies (eds). Blackwell Scientific Publications, Oxford.

Landless, P.J. 1976. Demand feeding behaviour of rainbow trout. Aquaculture 7:11-25.

Larkin, P.A., Anderson, G.C., Clemens, W.A. and Mackay, D.C.G. 1950. The production of Kamloops trout (Salmo gairdneri) in Paul Lake, B.C. Sci. Publs. B.C. Game Dept. no. 1. 37pp.

Le Cren, E.D. 1965. Some factors regulating the size of populations of freshwater fish. Mitt. Internat. Verein. Limnol. 13:88-105.

Lewontin, R.C. 1966. On the measurement of relative variability. Syst. Zool. 15:141-142.

Li, H.W. and Brocksen, R.W. 1977. Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (Salmo gairdneri). J. Fish. Biol. 11:329-341.

McFadden, J.T. 1969. Dynamics and regulation of salmonid populations in streams. Pp. 313-329 in Salmon and trout in streams. T.G. Northcote (ed.) H.R. Macmillan Lect. in Fisheries, Univ. British Columbia, Vancouver, B.C.

McNicol, R.E. and Noakes, D.L.G. 1984. Environmental influences on territoriality of juvenile brook charr, Salvelinus fontinalis, in a stream environment. Envir. Biol. Fishes 10:29-42.

MacPhee, C. 1961. An experimental study of competition for food in fish. Ecology 42:666-681.

Magnuson, J.J. 1962. An analysis of aggressive behaviour and competition for food and space in medaka (Oryzias latipes), Pisces, Cyprinodontidae. Can. J. Zool. 40:313-363.

Maher, F.P. and Larkin, P.A. 1955. Life history of the steelhead trout of the Chilliwack River. Trans. Am. Fish. Soc. 84:27-38.

Mason, J.C. 1966. Behavioural ecology of juvenile coho salmon (Oncorhynchus kisutch) in stream aquaria with particular reference to competition and aggressive behaviour. Ph.D. Thesis. Oregon State Univ., Corvallis. 195pp.

Mason, J.C. 1976. Response of underyearling coho salmon to supplementary feeding in a natural stream. J. Wildl. Manag. 40:775-788.

Mason, J.C. and Chapman, D.W. 1965. Significance of early emergence, environmental rearing capacity and behavioural ecology of juvenile coho salmon in stream channels. J. Fish. Res. Board Can. 22:173-190.

Maynard Smith, J. and Parker, G.A. 1976. The logic of asymmetric contests. Anim. Behav. 24:159-175.

Mazeaud, M.M., Mazeaud, F. and Donaldson, E.M. 1977. Primary and secondary effects of stress in fish: some new results data, with a general review. Trans. Am. Fish. Soc. 106:201-212.

Miller, R.B. 1958. The role of competition in the mortality of hatchery trout. J. Fish. Res. Board Can. 15:27-45.

Moring, J.R. 1982, Fin erosion and culture related injuries of chinook salmon raised in floating pens. Prog. Fish Cult. 44:189-191.

Moyle, P.B. 1969. Comparative behaviour of young brook trout of domestic and wild origin. Prog. Fish Cult. 31:51-59.

Newman, M.A. 1956. Social behaviour and interspecific competition in two trout species. Physiol. Zool. 29:64-81.

Noakes, D.L.G. 1978. Social behaviour as it influences fish production. Pp 260-282 in Ecology of freshwater fish production. S.D. Gerking (ed.) Blackwell, Oxford.

Noakes, D.L.G., and Leatherland, J.F. 1977. Social dominance and interrenal cell activity in rainbow trout, Salmo gairdneri (Pisces; Salmonidae). Env. Biol. Fish. 2:131-136.

Northcote, T.G. 1962. Migratory behaviour of juvenile rainbow trout, Salmo gairdneri, in outlet and inlet streams of Loon Lake, British Columbia. J. Fish. Res. Board Can. 19:201-270.

Novotny, A.J. 1980. Delayed release of salmon. Pp 325-369 in Salmon Ranching. J.E. Thorpe (ed.) Academic Press, New York.

O'Keefe, T.M., Purdy, C.B., Brauer, E.P. and Willoughby, C.E. 1979. A mechanical volumetric feeding device for aquaculture research. Aquaculture 17:69-71.

Parker, G.A. 1974. Assessment strategy and the evolution of animal conflicts. J. Theor. Biol. 47:223-243.

Parker, R.R. and Larkin, P.A. 1959. A concept of growth in fishes. J. Fish. Res. Board. Can. 16:721-745.

Peters, R.H. 1983. The ecological implications of body size. Cambridge Univ. Press, New York. 329 pp.

Puckett, K.J. and Dill, L.M. 1985. The energetics of feeding territoriality in juvenile coho salmon (Oncorhynchus kisutch). Behaviour. 92:91-111.

Ra'anan, Z. and Cohen, D. 1984. The effect of group interactions on the development of size distribution in Macrobrachium rosenbergii (De Man) junvenile populations. Biol. Bull. 166:22-31.

Refstie, T. and Steine, T.A. 1978. Selection experiments with salmon. II. Genetic and environmental sources of length and weight variation of Atlantic salmon in the freshwater phase. Aquaculture 14:221-234.

Rowell, T.E. 1974. The concept of social dominance. Behav. Biol. 11:131-154.

Rubenstein, D.I. 1981. Combat and communication in the everglades pygmy sunfish. Anim. Behav. 29:249-258.

Schneider, R. and Nicholson, B.L. 1980. Bacteria associated with fin rot disease in hatchery reared Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 37:1505-1513.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:370-404.

Schoener T.W. 1983. Simple models of optimal territory size: a reconciliation. Am. Nat. 121:608-629.

Schuck, H.A. 1948. Survival of hatchery trout in streams and possible methods of improving the quality of hatchery trout. Prog. Fish Cult. 10:3-14.

S.E.P. Annual Report. 1979. M. Glover and J Barnetson. (eds). Govt. of Canada. 92pp.

Shelborn, J.E., Brett, J.R. and Shirahata, S. 1973. Effect of temperature and feeding regime on the specific growth rate of sockeye salmon fry (Oncorhynchus nerka), with a consideration of the size effect. J. Fish. Res. Board Can. 30:1191-1194.

Shelton, W.L., Davies, W.D., King, T.A. and Timmons, T.J. 1979. Variation in growth of the initial year class of largemouth bass in Westpoint Res. Alabama and Georgia. Trans. Am. Fish. Soc. 108:142-149.

Shirahata, S. 1964. On "cannibalism" in rainbow trout fingerling, Salmo gairdneri irideus. Jap. J. Ecol. 14:25-32.

Slaney, P.A., and Harrower, W.L. 1981. Experimental culture and release of steelhead trout reared in net pens at O'Connor Lake in British Columbia. Pp 43-49 in Proceeding: propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat symposium. October 15-17, Humboldt State University, Arcata, California.

Slaney, P.A. and Northcote, T.G. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout in laboratory stream channels. J. Fish. Res. Board Can. 31:1201-1209.

Sosiak, A.J., Randall, R.G. and McKenzie, J.A. 1979. Feeding by hatchery reared and wild Atlantic salmon. J. Fish. Res. Board Can. 36:1408-1412.

Stringer, G.E. and Hoar, W.S. 1955. Aggressive behaviour of underyearling Kamloops trout. Can. J. Zool. 33:148-160.

Symons, P.E.K. 1968. Increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food. J. Fish. Res. Board Can. 25:2387-2401.

Symons, P.E.K. 1971. Behavioural adjustment of population density to available food by juvenile Atlantic salmon. J. Anim. Ecol. 40:569-587.

Symons, P.E.K. 1974. Territorial behaviour of juvenile Atlantic salmon reduced predation by brook trout. Can. J. Zool. 52:677-679.

Teitelbaum, P. 1966. Motivation and control of food intake. Pp 319-335 in Handbook of physiol. Am. Physiol. Soc., Washington.

Tinbergen, N. 1951. The study of instinct. Oxford University Press, New York, 228pp.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (Salvelinus fontinalis Mitchell). Trans. Am. Fish. Soc. 89:25-32.

Wade, T.D. 1978. Status and hierarchy in nonhuman primate societies. Pp 109-134 in Perspectives in Ethology, Vol. 3, P.P.G. Bateson and P.H. Klopfer (eds). Plenum Press, New York.

Wankowski, J.W.J., and Thorpe, J.E. 1979. Spatial distribution and feeding in Atlantic salmon, Salmo salar L., juveniles. J. Fish Biol. 114:239-247.

Weatherly, A.H. and Rodgers, S.C. 1978. Some aspects of age and growth. Pp 52-74 in The ecology of freshwater fish production, S.D. Gerking (ed.) Blackwell, Oxford.

Webb, P.W. 1978. Partitioning of energy into metabolism and growth. Pp 184-214 in The ecology of freshwater fish production, S.D. Gerking (ed.) Blackwell, Oxford.

Whitlock, D. 1974. Fish stocking and reproduction: trout and warmwater species. Pp 123-153 in The Stream Conservation Handbook, J.M. Migel (ed.) Crown Publishers Inc, New York.

Wilson, E.O. 1975. Sociobiology: the new synthesis. Belknap Press, Cambridge, Mass. 697pp.

Yamagishi, H. 1962. Growth relations in some small experimental populations of rainbow trout fry, Salmo gairdneri, Richardson, with special reference to social relations among individuals. Jap. J. Ecol. 12:43-53.

Yamagishi, H. Matsushima, T. and Nakamura M. 1981. Note on the aggressive behaviour of juvenile Japanese chum salmon, Oncorhynchus keta (Walbaum). Sci. Repts. Hokkaido Salmon Hatchery 35:25-31.